

Geographical variation in Slate-crowned Antpitta *Grallaricula nana*, with two new subspecies, from Colombia and Venezuela

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Slate-crowned Antpitta *Grallaricula nana* is a small member of the Grallariidae found in the northern Andes. The song of most populations has been sound-recorded (Appendix 1) and some ecological data have been published (Delgado 2002, Greeney & Sornoza 2005, Greeney *et al.* 2008, Niklison *et al.* 2008), but no detailed revision of its taxonomy has been attempted. Six subspecies of *G. nana* have been described from eastern Venezuela to northern Peru, with a disjunct population in the tepui region of southern Venezuela and Guyana (Krabbe & Schulenberg 2003). Subspecies are considered separable by the extent of white on their otherwise red-orange underparts, the colour saturation of the underparts and upperparts and eye-ring pattern (Figs. 1–7). It has recently been suggested that one of the Venezuelan populations might warrant species rank based on plumage and voice (Ridgely & Tudor 1994, Boesman 1999). Separately, recent range extensions (i.e. new populations) in Colombia (Andrade & Lozano 1997, Salaman *et al.* 2002, Cuervo *et al.* 2003, Krabbe *et al.* 2006, Echeverry & Córdoba 2007, Donegan *et al.* 2007) mandate a re-evaluation of subspecific taxonomy. In particular, the nominate subspecies has recently been considered to encompass all Andean populations from Venezuela to Peru (Krabbe & Schulenberg 2003), but published voice recordings (Appendix 1; Figs. 10–12) evidence substantial geographical variation within this region.

Grallaricula is currently treated, together with most other antpitta genera, in the family Grallariidae (Irestedt *et al.* 2002, Chesser 2004, Rice 2005a,b, Remsen *et al.* 2008). Many species of antpitta occur in montane regions, and individuals probably possess poor dispersal abilities, being unable to cross low valleys of unsuitable habitat. *Grallaricula* are secretive understory birds that are more frequently heard than seen. Within the Neotropics, these factors have contributed to the family probably being second only to Rhinocryptidae in the number of new taxa described recently, as previously unknown populations have been discovered and sound-recorded (Graves *et al.* 1983, Graves 1987, Schulenberg & Williams 1992, Stiles 1992, Krabbe *et al.* 1999).

Two subspecies of *G. nana* are described from Colombia: *G. n. nana* (Lafresnaye, 1842) and *G. n. occidentalis* Todd, 1927. The latter was recently considered a synonym of the nom-

Captions to figures on opposite page

Figure 1. *G. n. hallsi* holotype, Serranía de los Yariagués, Colombia, January 2005 (Blanca Huertas / Proyecto EBA)

Figure 2. Immature *G. n. nanitaea*, Suratá, dpto. Santander, Colombia (Jorge E. Avendaño-C.)

Figure 3. *G. n. pariae*, Cerro Humo, Sucre, Venezuela (Joseph A. Tobias)

Figure 4. BMNH specimens, showing geographical variation in *G. nana*, from left to right: (i) *G. n. pariae* (1951.1.2, formerly COP 44254, paratype); (ii) *G. n. kukenamensis* (89.7.10.926, holotype); (iii) *G. n. olivascens* (1915.3.16); (iv) *G. n. nana* (89.9.10.927); and (v) *G. n. occidentalis* (89.7.10.956) (Thomas M. Donegan, © Natural History Museum, Tring)

Figure 5. ICN specimens, from left to right: (i) *G. n. occidentalis* West Andes population (25920); (ii) *G. n. nana* (31322); (iii) *G. n. hallsi* (35555, paratype); (iv) *G. n. hallsi* (35195, holotype); (v) *G. n. hallsi* (35193, paratype) and (vi) *G. n. nanitaea* Tamá population (33933, formerly IAVH 10645) (Thomas M. Donegan)

A



1B



3



5





Figure 6. Series at BMNH showing differences in underparts plumage saturation between *G. n. nana* and *G. n. occidentalis*: at left five *G. n. nana*, from left to right (i) 44.12.31.21, (ii) 89.9.20.652, (iii) 89.9.20.651, (iv) 54.1.25.81, (v) 89.9.10.927; at right three *G. n. occidentalis*, from left to right (vi) 89.7.10.956, (vii) 89.7.10.929, and (viii) 89.7.10.928 (Thomas M. Donegan, © Natural History Museum, Tring)



Figure 7. AMNH series of *G. n. nanitaea*, left to right: (i) 96305 (paratype); (ii) 492316; (iii); 146661 (holotype); (iv) 100209; (v) 492312; (vi) 492311; (vii) 492313; (viii) 492318; (ix) 492315; (x) 492317 (paratype); and (xi) 492314 (Thomas M. Donegan)

Figure 8. Bill morphology of (left to right): (i) *G. n. olivascens* BMNH 1915.3.16; (ii) *G. n. kukenamensis* BMNH 89.7.10.926; and (iii) *G. n. pariae* BMNH 1951.1.2 (Thomas M. Donegan, © Natural History Museum, Tring)



inate because West Andean and Ecuadorian specimens possess similar plumage (Krabbe & Schulenberg 2003). The other described subspecies all occur in Venezuela and Guyana: *G. n. olivascens* Hellmayr, 1917, of the Coastal Cordillera, *G. n. cumanensis* E. J. O. Hartert, 1900 of the Caripe Mountains, *G. n. pariae* Phelps & Phelps Jr., 1949, of the Paria Peninsula, and *G. n. kukenamensis* Chubb, 1918, of the tepuis.

Methods

Specimens of *G. nana* and other *Grallaricula* species were studied at the following institutions: American Museum of Natural History, New York (AMNH); Natural History Museum, Tring (BMNH); Colección Ornitológica Phelps, Caracas (COP); Instituto Alexander von Humboldt, Villa de Leyva, Colombia (IAVH); Instituto de Ciencias Naturales, Universidad Nacional, Bogotá (ICN); Museo de Historia Natural, Universidad de la Salle, Bogotá (MLS); and Muséum National d'Histoire Naturelle, Paris (MNHN). Details of other Colombian specimens were taken from Project Biomap (www.biomap.net). Photographs of specimens in the Biomap database held at the following museums were studied: Academy of Natural Sciences, Philadelphia (ANSP); Carnegie Museum of Natural History, Pittsburgh (CM); Museum of Comparative Zoology, Cambridge, MA (MCZ); Field Museum of Natural History, Chicago (FMNH); and Los Angeles County Natural History Museum (LACM). A list of specimens inspected and their localities, which includes type specimens of almost all taxa, is presented in Appendix 1.

The following measurements were taken for each specimen: wing-chord and tail length (to nearest 0.5 mm), tarsus length, culmen length from skull to tip of upper mandible and bill width at mid-point of the nostrils (to nearest 0.5 mm) and, from specimen labels, mass (g) data were also obtained. Data from birds in juvenile plumage, moulting from juvenile to adult plumage, or otherwise in moult were excluded from analyses. Juvenile and immature specimens are easily identified in *G. nana* by the presence of patchy dark rufous feathering. Due to time constraints and the number of specimens, only a sample of *G. n. pariae* material at COP was measured, but others were inspected. Biometric data are presented in Appendix 2.

Vocalisations in suboscines, such as *Grallaricula*, are considered innate and stereotypical (Kroodsma 1984), and in another high-elevation Andean suboscine genus, *Scytalopus*, these provide a better reflection of molecular differences than plumage characters (Arcander & Fjeldså 1994). Vocal differences between populations may therefore have a genetic basis and can inform taxonomy (e.g. Isler *et al.* 1997, 1999, 2006, 2007, 2008, Krabbe & Schulenberg 1997). To assess taxon rank, a combination of morphological and vocal evidence is often considered helpful under a modern interpretation of the Biological Species Concept (Helbig *et al.* 2002).

Published and unpublished sound-recordings of *G. nana* were studied. For comparison, Venezuelan recordings of nominate Rusty-breasted Antpitta *G. ferrugineipectus*, Crescent-faced Antpitta *G. lineifrons* and presumed recordings of Hooded Antpitta *G. cucullata* were also studied (Appendix 3). These taxa were chosen because they have structurally similar songs to *G. nana* taxa and do not present significant taxonomic issues (*cf.* Ecuadorian and Colombian *G. ferrugineipectus*). Sonograms were generated using the default settings of Raven Lite 1.0, sometimes adjusted for brightness and expanded to show at least the detail in Figs. 10–12. Audacity 1.2.6 was used to remove 'noise' from some recordings. Both the loudsong (*sensu* Willis 1967, hereafter 'song') and calls were analysed. Data from songs that were curtailed (e.g. *G. n. olivascens*) were ignored. If calls were combined with songs, or elaborate introductory or terminating sequences were included with songs (e.g. some recordings of *G. lineifrons* and *G. ferrugineipectus*), such calls or sequences were excluded. Songs and calls were defined as sequences of notes broken by gaps significantly longer than the intervals between individual notes of a sequence. Multiple songs and calls were measured from single recordings and localities, where available, to determine the full range of variables. Recordings of individuals under natural conditions and after playback were

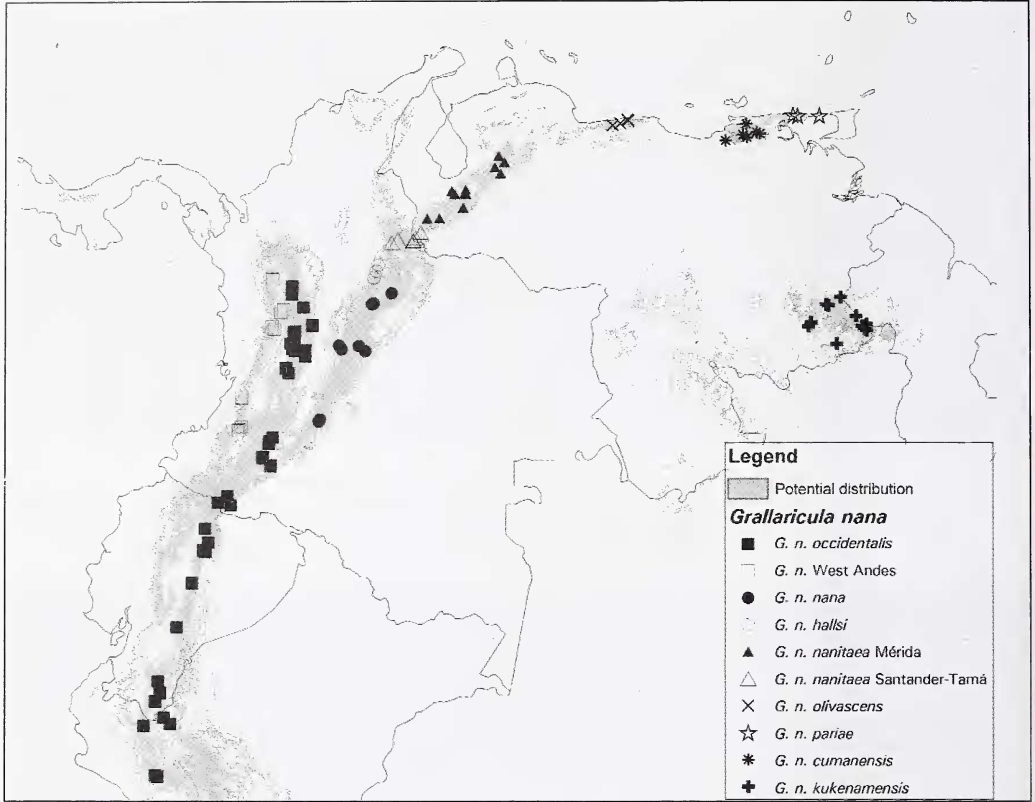
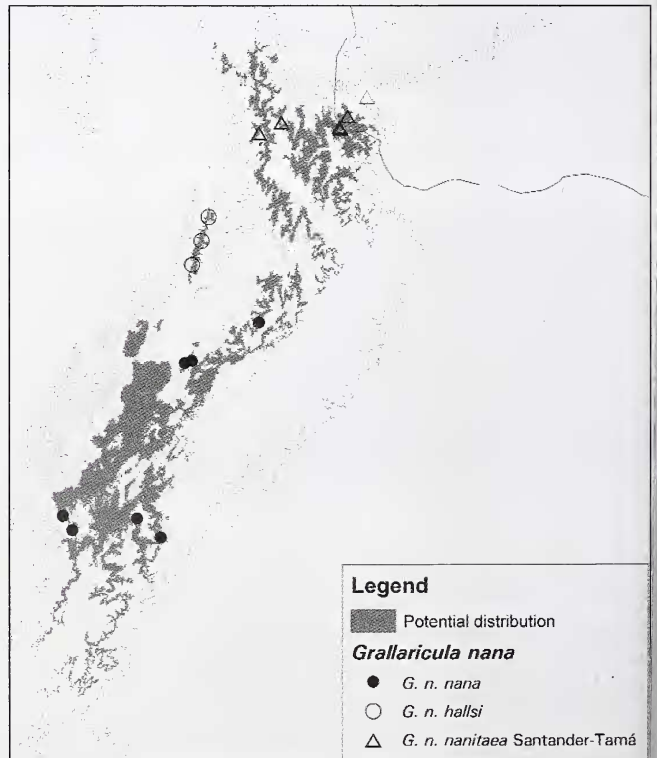


Figure 9. Potential distribution maps using MAXENT 3.0 (Phillips *et al.* 2006) based on topography and climate layers available from Worldclim (Hijmans *et al.* 2005) showing records of *G. nana* taxa.

A (above). All *G. nana* populations. Potential distribution is based on three analyses: (i) *nana* group; (ii) *cumanensis* group; and (iii) *kukanamensis*. The potential range of the species includes unsuitable sites (e.g. west slope of the Andes in Ecuador and lower elevations) probably due to inaccurate locality data for older specimens.

B (right). Three Eastern Cordillera *G. nana* taxa only, including the two new subspecies described in this paper.



included for the same reason. Data on numbers of recordings and sonograms are presented for each taxon in Appendix 3. Appendix 1 contains a gazetteer of recording localities.

Various vocal variables described by Isler *et al.* (1997, 1999, 2006, 2007, 2008) were considered for further analysis during a preliminary study of sonograms. Variables that showed variation between populations were analysed further, whilst apparently constant variables and those inappropriate for study were not. For example, as calls and songs comprise a number of individual notes at the same volume but different acoustic frequency, acoustic frequency variables defined with reference to a 'principal' note were not amenable to study. Measurements of frequency bandwidth were avoided because individual notes in the songs of several populations show short, quiet 'tails' on sonograms (Figs. 10–11), meaning that the lowest or highest recorded point is biased by the quality of the recording equipment and distance of the bird from the microphone. The maximum point of the note excluding such tails, or the maximum point of an up–down stroke, provide a more consistent reference point for these birds. Finally, calls of *G. n. pariae* and *G. n. cumanensis* comprise a series of fast trills, which were analysed separately, both for series of trills and for each individual trill.

Data for the following variables were analysed: (i) number of notes in song; (ii) total song duration (seconds); (iii) mean number of notes per second (by dividing i and ii); (iv) maximum acoustic frequency of highest note (kHz); (v) maximum acoustic frequency of lowest note (kHz); (vi) variation in acoustic frequency (kHz) (by calculating iv minus v); (vii) time of peak in frequency (measured from the start of the song until the midpoint of the highest frequency—if various notes shared the peak frequency the middle note was used); (viii) position of peak within call (calculated as vii divided by ii); (ix) note length at start (time from the start of the second note to the start of the third, ignoring 'rasping' notes); (x) note length at end (time from the start of the penultimate note to the start of the last, ignoring 'rasping' notes); (xi) change of pace (calculated as viii divided by ix); and (xii) subjective description of individual note shape. Individual notes in songs generally appear as 'blobs' or up–down strokes (chevrons). 'Blobs' were often skewed into a rounded parallelogram or u / n shape, and were classed as flat (no or marginal skew), up (left side lower than right), down (left side higher than right), 'n' ('tails' of decreasing frequency at start and end) or 'u' ('tails' of increasing frequency at start and end).

Of these variables, the following were discarded as being correlated with or dependent upon other variables: (v), (vii), (ix) and (x). For diagnosability analyses (Appendix 4) and mean and standard deviation (Appendix 3), a reduced dataset comprising the first three sonograms with complete data available for each recording was used. An edited dataset alone was compiled for those species studied only for comparative purposes.

To analyse species and subspecies limits, biometric and vocal data were subdivided on the basis of plumage differences and well-known biogeographic regions for montane birds: (i) tepuis; (ii) Paria Peninsula, Venezuela; (iii) Caripe Mountains, Venezuela; (iv) Coastal Cordillera, Venezuela; (v) Mérida Andes, Venezuela; (vi) Tamá–Santander region, northern East Andes of Colombia; (vii) Serranía de los Yariguíes, East Andes, Colombia; (viii) East Andes of Colombia north of the Picachos depression; (ix) East Andes of Colombia south of the Picachos depression; (x) 'Nudo de Pasto' region in dptos. Cauca / Huila where Central and East Andes join; (xi) Central Andes, Colombia north of dpto. Huila; (x) West Andes, Colombia; (xii) Ecuador and Peru (subdivision into Ecuador and southern Ecuador / Peru recordings having revealed no vocal differences).

Statistical tests.—Various diagnosability tests were made for pairs of vocal and biometric variables of these populations, as follows.

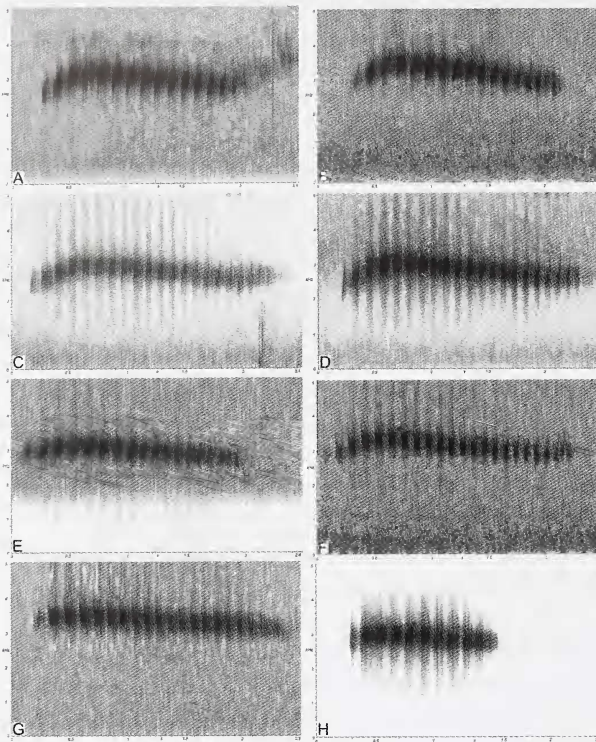


Figure 10. Sonograms of songs of Colombian, Ecuadorian and Peruvian *G. nana* populations: (a) *G. n. occidentalis* (Cabañas San Isidro, Ecuador: N. Athanas: XC 5060); (b) *G. n. occidentalis* (Cerro Chinguela, Peru: T. A. Parker *in* Isler & Whitney 2002); (c) *G. n. occidentalis* (Rogitama, Colombia: M. Álvarez: IAVH 10442); (d) *G. n. nana* (Serranía de los Picachos, Colombia: Álvarez 2000); (e) *G. n. occidentalis* (Río Blanco, Caldas: Álvarez & Córdoba 2000); (f) *G. n. occidentalis* population in West Andes (Páramo Frontino, Colombia: N. Krabbe); (g) *G. n. nanitaea* Tamá, Colombia (Córdoba & Álvarez 2003); (h) *G. n. hallsi* (Serranía de los Yariquíes, Colombia: T. M. Donegan: XC 21498), with noise removal using Audacity.

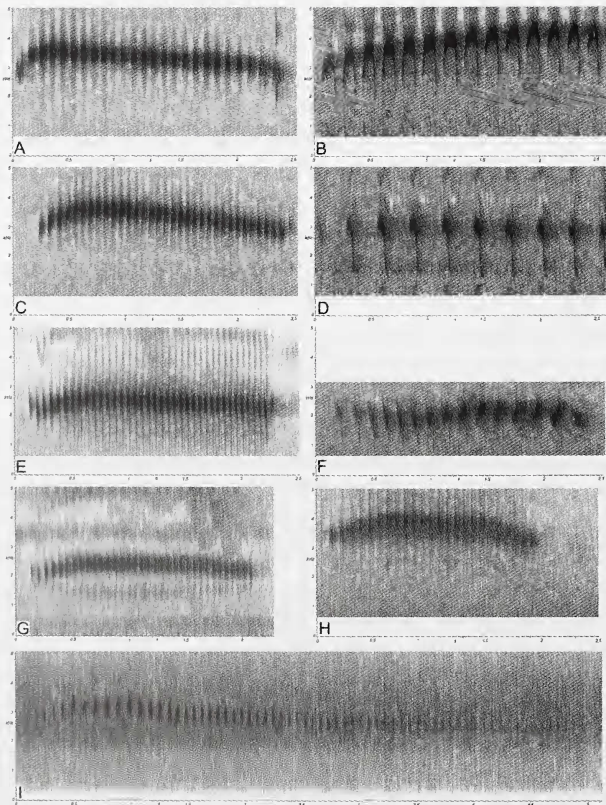


Figure 11. Sonograms of songs of Venezuelan subspecies of *G. nana* (at left) and other *Grallaricula* species (right): (a) *G. n. nanitaea* Mérida (Páramo Zumbador: P. Schwarz); (b) *G. lineifrons* (Cerro Mongus, Carchí, Ecuador: Krabbe & Nilsson 2003); (c) *G. n. olivascens* (Colonia Tovar: P. Schwarz); (d) *G. ferrugineipectus* (Utuaña, Loja, Ecuador: Krabbe & Nilsson 2003); (e) *G. n. cumanensis* (Piedra de Moler: C. A. Marantz); (f) *G. f. ferrugineipectus* (Serranía de San Luis, Venezuela: Boesman 1999); (g) *G. n. pariae* (Paria Peninsula: Boesman 1999); (h) probable *G. cucullata* (upper río Yurayaco, Colombia: M. Álvarez: IAVH 4260); (i) *G. n. kukenamensis* (upper Escalera: P. Boesman, recording identified as '80%' certain). Some frequency bandwidths removed to delete calls of other species and low-frequency 'noise'.

LEVEL 1: statistically significant differences at $p < 0.05$. A Bonferroni correction was applied for both vocal data (seven variables) and biometrics (five variables), to produce $p < 0.0071$ and $p < 0.01$ respectively. For biometrics, acoustic frequency and other primary data, an unequal variance (Welch's) t -test was used; for speed and other derived or ratio data, both Kolmogorov-Smirnov and Mann-Whitney U tests were also applied to account for any non-normal distributions. The Level 1 calculation assesses statistical significance, but tolerates considerable overlap. Further calculations, described below, were undertaken to measure inter-population differences in the context of various species and subspecies concepts. In the formulae used below, \bar{x}_1 and s_1 are the sample mean and sample standard deviation of Population 1; \bar{x}_2 and s_2 refer to the same parameters in Population 2; and the t value uses one-sided confidence intervals at the percentage specified for the lower degree of freedom of the two populations for the relevant variable, with t_1 referring to Population 1 and t_2 referring to Population 2.

LEVEL 2: a '50% / 97.5%' test, following Hubbs & Perlmutter's (1942) now little-used subspecies concept, which is passed if sample means are two standard deviations or more apart, here defined as the sample mean of Population 1 falling outside the range of 97.5% of Population 2, controlling for sample size: $|(\bar{x}_1 - \bar{x}_2)| > (s_1(t_{1@97.5\%}) + s_2(t_{2@97.5\%}))/2$.

LEVEL 3: The traditional '75% / 99%' test for subspecies (Amadon 1949, Patten & Unitt 2002), modified to control for sample size: $|(\bar{x}_1 - \bar{x}_2)| > s_1(t_{1@99\%}) + s_2(t_{2@75\%})$ and $|(\bar{x}_2 - \bar{x}_1)| > s_2(t_{2@99\%}) + s_1(t_{1@75\%})$.

LEVEL 4: diagnosability based on recorded values (first part of Isler *et al.*'s 1999 diagnosability test).

LEVEL 5: so-called '95% / 95%' diagnosability (i.e. 97.5%/97.5%, given that the lower 2.5% of each population is also outside the range of each population). This occurs when sample means are four standard deviations apart, controlling for sample size, and is the second part of Isler *et al.*'s (1999) diagnosability test: $|(\bar{x}_1 - \bar{x}_2)| > s_1(t_{1@97.5\%}) + s_2(t_{2@97.5\%})$

For one taxon (*G. n. kukenamensis*) only a single sound-recording of the song and call was available (Fig. 11i), and this was identified with only 80% certainty by the recordist (P. Boesman *in litt.* 2008), based on its locality and resemblance in structure to *Grallaricula* songs. Songs of all other Grallaridae in the tepuis are known and none of those persons that is familiar with tepui avifauna consulted has proffered an alternative identification. The single-note call given prior to the song (Fig. 12m) also coincides with Braun *et al.*'s (2003) description and is similar to the single-note calls given by other *G. nana* taxa. However, the recording differs from unpublished recordings that are certainly of *G. n. kukenamensis* and which will be published elsewhere (D. Ascanio *in litt.* 2008), suggesting that *G. n. kukenamensis* may possess different calls. The following formulae were used to assess diagnosability of this single recording, where y is the relevant value for the *G. n. kukenamensis* recording; \bar{x}_1 and s_1 are the sample mean and sample standard deviation of the compared population; and the t value uses one-sided confidence intervals at the percentage specified for the lower degree of freedom of the two populations for the relevant variable. The tests were based on the assumption that the recording is of an individual with an unusual song at the highest or lowest 2.5 percentile for each variable studied: Level 2: $y < \bar{x}_1 - 2s_1t_{1@97.5\%}$ or $y > \bar{x}_1 + 2s_1t_{1@97.5\%}$. Level 4: diagnosability based on recorded values; Level 5: $y < \bar{x}_1 - 3s_1t_{1@97.5\%}$ or $y > \bar{x}_1 + 3s_1t_{1@97.5\%}$.

Helbig *et al.* (2002) suggested that, to assess the rank of allopatric populations, a comparison with closely related sympatric or parapatric populations known to be species should be undertaken. Isler *et al.* (1999) suggested assigning species rank to allopatric Thamnophilidae populations where three or more measured vocal variables for loudsongs differed diagnosably, based on observed differences between closely related sympatric

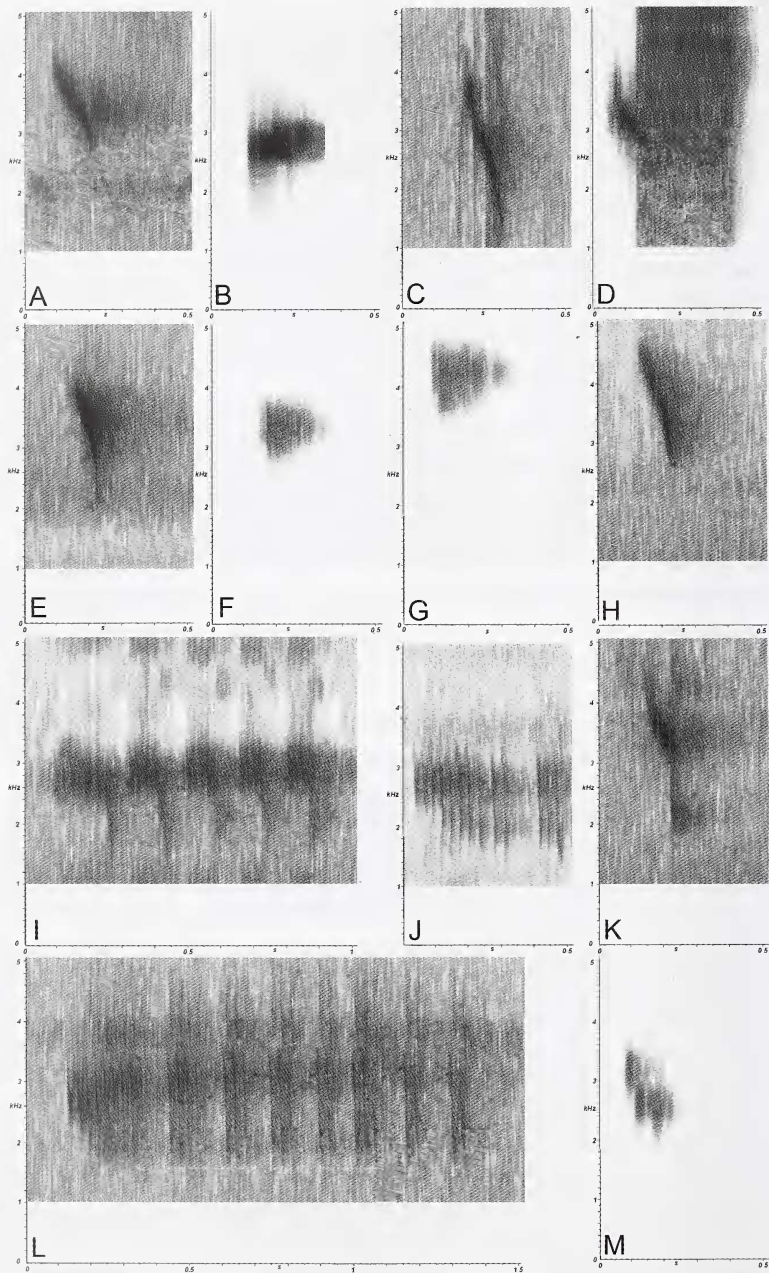


Figure 12. Sonograms of scolds of *G. nana* taxa: (a) *G. n. occidentalis* (Río Blanco, Caldas, Colombia: D. Calderón: XC 'Mystery' 300); (b) *G. n. occidentalis* (as A, XC 'Mystery' 306); (c) *G. n. hallsi* (holotype, Lepipuerto, Yariquíes, Colombia: T. M. Donegan: XC 21508); (d) *G. n. hallsi* (as C, in-hand distress call: T. M. Donegan: XC 21507); (e) *G. n. occidentalis* (Guacamayos, Napo, Ecuador: Krabbe *et al.* 2001); (f) apparent *G. n. nana* (Parque Nacional Natural Picachos, Caquetá, Colombia: M. Álvarez: IAVH 345); (g) apparent *G. n. nanitaea* (Tamá, Norte de Santander, Colombia: M. Álvarez: IAVH 11722); (h) *G. n. nanitaea* (Universidad de los Andes, Mérida, Venezuela: K. J. Zimmer); (i) *G. n. cumanensis* (Cerro Negro, Sucre, Venezuela: Boesman 2007); (j) *G. n. pariae* (Cerro Humo, Sucre, Venezuela: R. Innes); (k) *G. n. olivascens* (Colonia Tovar, Aragua, Venezuela: M. L. Isler); (l) *G. n. pariae* (Cerro Humo, Sucre, Venezuela: J. I. Areta); (m) *G. n. kukenamensis* (upper Escalera, Venezuela: P. Boesman, recording identified as '80%' certain). Recordings b, d, f, g and m with noise removal by Audacity.

species in that family. For Rhinocryptidae, a single diagnostic vocal difference separated sympatric taxa (Donegan & Avendaño-C. 2008). Various comparisons between sympatric or parapatric *Grallaricula* populations were undertaken. Isler *et al.*'s (1999) diagnosability tests (Levels 4 and 5, or for note shape Level 4) together with my test of statistical significance (Level 1) were met for: (i) nominate *G. ferrugineipectus* vs. Mérida Andes *G. nana* (three variables: song speed, highest frequency and position of peak in frequency); (ii) *G. lineifrons* vs. Ecuadorian *G. nana* (four variables: song speed, highest frequency, position of peak in frequency and note shape); and (iii) *G. cucullata* vs. *G. nana* in the East Andes of Colombia (three variables: song speed, highest frequency and note shape). I therefore propose ranking allopatric *Grallaricula* populations as biological species where they show Levels 1, 4 and 5 diagnosability (or Level 4 for note shape) for three or more variables in songs.

For subspecies, Isler *et al.* (2006, 2007) suggested a 'full diagnosability for one character' test (whether vocal, biometrics or plumage) to diagnose subspecies of *Thamnophilidae* (Level 4/5 for at least one variable: essentially a phylogenetic species with small differences). The traditional test in ornithology for diagnosing subspecies is the Level 3 '99%/75%' test. Stiles & Caycedo (2002) ranked an allopatric population with statistically significant means for different variables (my Level 1) subspecifically. Where allopatric populations meet Levels 1, 3 and 4/5 for at least one character (i.e. satisfy all subspecies definitions), I conservatively describe them as subspecies, and I propose synonymy only if allopatric populations fail to achieve any level of diagnosability (i.e. do not pass any subspecific definitions). Other putative subspecies are discussed but not described. This approach may produce inconsistency, because historically recognised but dubious taxa maintain their status, but similarly differentiated undescribed populations continue to lack nomenclatural status. However, this approach results in a high threshold for both new taxa and synonymisation treatments, thereby maintaining current taxonomic treatments for other populations pending molecular or other studies.

Geographical variation in the northern Andes

The Andean races *G. n. nana* and *G. n. occidentalis* present a taxonomic challenge due to the provenance of their types. Here, I briefly discuss geographical variation in *G. nana* in the northern Andes, before going on to assign available names to those populations to which they apparently refer. Specimen and vocal studies (see Appendices) suggest that the following populations within *G. n. nana* are differentiated to varying degrees, from west to east and south to north in turn. Differences are illustrated in Figs. 1–7.

(i) WEST ANDES.—Records in dptos. Cauca, Valle, Risaralda and Antioquia (Cuervo *et al.* 2003, Krabbe *et al.* 2006). A small white chest collar is present on many specimens, a feature reduced in adjacent regions. This population may show small differences in dorsal plumage between (paler) Central Andes and (darker) East Andes specimens (Fig. 5), but this is tentative and Central Andes / Ecuador specimens exhibit some variation in upperparts plumage. The song differs (mostly Level 1) from other Colombian populations in its duration, greater number of notes, greater frequency variation and greater change of pace (Appendix 4). The call is not known.

(ii) CENTRAL ANDES / ECUADOR / PERU.—Records in dptos. Caldas, Risaralda, Quindío and Antioquia, Colombia (Hilty & Brown 1986). In Ecuador and Peru, it occurs along the entire east slope south to dpto. Cajamarca (Fjeldså & Krabbe 1990, Ridgely & Tudor 1994, Ridgely & Greenfield 2001, Schulenberg *et al.* 2007). Specimens have on average paler, more orange underparts than those in the East Andes, and no significant white breast collar is evident (Fig. 6). The song in the Central Andes has been considered 'more

plaintive' than in Ecuador (Krabbe & Schulenberg 2003), but my sample reveals the recording on which this comment was based (Álvarez & Córdoba 2002; Fig. 10e) to be atypical in acoustic frequency variation. Only small but statistically significant differences in acoustic frequency and bill width are evident between Central Andean and Ecuadorian populations, which are not separated by any known ecological divide. I found no differences in plumage or song between Central Andes and Ecuadorian populations.

(iii) EAST ANDES.—Records in dptos. Cundinamarca and Boyacá, Colombia (Andrade & Lozano 1997, Salaman *et al.* 2002). Populations in Serranía de los Picachos, Caquetá, are indistinguishable in plumage and vocals from those north of the Picachos depression (Appendices 2–3). This population has rather dark or ferruginous underparts and a brown-er back than those further north and east (Figs. 4–6). Recent studies in the East Andes and an ICN specimen (Andrade & Lozano 1997) confirm that most of the rather dark-breasted 'Bogotá' specimens refer to this taxon. The song and calls are of lower frequency than Central Andes, West Andes and more northern populations (except Yariguíes) (Figs. 10 and 12). A population at the head of the Magdalena Valley and Nudo de Pasto in dptos. Cauca and Huila, and on the east slope of the Andes in dpto. Nariño is geographically continuous with the Central Andes / Ecuador / Peru population but appears to show some 'bleeding' of morphological and vocal features of the East Andes, with on average darker underparts and lower frequency songs in this region.

(iv) SERRANÍA DE LOS YARIGUÍES.—A population recently discovered in this isolated mountain range of the East Andes, in Colombia, is described below.

(v) TAMÁ-SANTANDER.—Records in Colombia and Venezuela in Tamá National Park (Hilty & Brown 1986), with recent specimens from nearby on the west slope of the East Andes at Suratá, dpto. Santander (J. Avendaño-C.). Plumage is similar to that of birds in Serranía de los Yariguíes, but the song is higher frequency (Level 5) than other East Andean populations and is longer and faster on average.

(vi) VENEZUELAN ANDES.—Plumage and voice are similar to the Tamá population, but the song is faster and longer on average. No diagnostic differences in voice or plumage are evident from the Tamá-Santander population. This population is described below.

The absence of *G. nana* in the Perijá range requires further investigation given the many other populations discovered recently, and the lack of field work incorporating mist-netting and sound-recording in that region.

Assignment of existing subspecies names to relevant populations

G. n. nana was described from a 'Colombie' skin by Lafresnaye (1842). The type (MCZ 76739) has a rather brown back, no white breast collar and a dark orange breast. Todd's (1927) notes are also consistent with the type being darker breasted than birds from the Central Andes that he described as *G. n. occidentalis*, apparently through direct comparison. *G. n. nana* thus probably refers to the main East Andes population. The type of *G. n. nana* could conceivably be from the head of the Magdalena valley or West Andes based on its plumage, but the hypothesis that it is an East Andes bird is not rejected.

G. n. occidentalis was purportedly described from the West Andes of Colombia (Todd 1927). However, the type locality is 'Sancudo' (=Zancudo), in the Central Andes (c.05°41'N, 75°07'W: Paynter & Traylor 1981). Todd also mentioned three specimens at CM from the West Andes that he did not designate as types, but the only three Colombian *G. nana* presently at CM were collected by Carriker at Sancudo. Todd's description of the plumage of *G. n. occidentalis* is consistent with other Central Andes skins, which are rather pale-

breasted compared to East Andes birds. *Contra* almost all literature, *G. n. occidentalis* therefore refers to the Central Andes population.

Krabbe & Schulenberg (2003) held *G. n. occidentalis* to be a synonym of *G. n. nana* on the basis of paler breasted birds in northern Peru similar to *G. n. occidentalis*. Although Central Andes and Ecuador / Peru populations are indistinguishable by voice or plumage, *G. n. nana* refers to the East Andes population. Intermediates appear to be present in Nudo de Pasto, but the Central Andes to Peru population and East Andes population are otherwise separable by plumage, and show Level 1/2 (Ecuador / Peru) and 1/2/3 (Central Andes) differences in acoustic frequency of their songs. Though insufficient to describe a new subspecies under the conservative approach adopted here, *G. n. occidentalis* can be maintained under '75%' subspecies concepts (e.g. Patten & Unitt 2002).

West Andean *G. nana* exhibit small plumage differences from *G. n. occidentalis* but no vocal variables are diagnostic. It was impossible to make adequate comparisons between specimens to determine if any diagnosable plumage differences exist, due to the relative lack of relevant material at any single institution, and the difficulty of importing and exporting biological material from Colombia. For now, the West Andes population is provisionally treated within *G. n. occidentalis*, but requires further investigation given that the West Andean range is isolated, shows considerable climatic differences from the Central Andes and is a centre of avian endemism (e.g. Salaman *et al.* 2003).

It is evident that at least two *G. nana* populations meet the level of all modern subspecies and pattern-defined species concepts: (i) Serranía de los Yariguíes; and (ii) Mérida-Tamá. These are described below.

Grallaricula nana hallsi subsp. nov.

Holotype.—Instituto de Ciencias Naturales, Universidad Nacional, Bogotá, Colombia (ICN 35195). Adult female collected by T. M. Donegan in montane forest just below the treeline at Lepipuerto, upper río Chimera, on the west slope of Serranía de los Yariguíes, Simacota or El Carmen municipality, dpto. Santander, Colombia (06°28'N, 73°28'W) at 2,900 m, on 10 January 2005. DNA sample, field no. 28C, is held at Instituto Alexander von Humboldt's molecular laboratory in Cali. A sound-recording of the holotype in the hand is available at www.xeno-canto.org; XC 21507–508.

Paratypes.—ICN 35193 is an adult female collected by T. M. Donegan on 8 January 2005 at the type locality. ICN 35555 is an adult female collected by T. M. Donegan and J. E. Avendaño-C. at La Aurora, east slope of Serranía de los Yariguíes, Galán municipality, dpto. Santander (06°38'N, 73°24'W) at 2,700 m, on 9 July 2006. An adult was trapped but not collected by J. E. Avendaño-C., at Alto Cantagallos, west slope of Serranía de los Yariguíes, San Vicente de Chucurí municipality, dpto. Santander (06°49'N, 73°22'W) at 2,450 m, in November 2006. Sound-recordings of songs of *G. nana* from the type locality are available at XC 21498–21506.

Diagnosis.—Referred to the genus *Grallaricula* by its diminutive size for a Grallariidae (wing 60–68 mm). Upperparts brownish or olivaceous, the pileum cinereous or rufous; entire underparts ferruginous-red or pale cinereous, the feathers sometimes fringed black; tail about one-third length of wing; and conspicuous rictal bristles (Lowery & O'Neill 1969). Referred to *G. nana* by its slaty crown, rufous underparts, olivaceous back, biometrics (Appendix 2) and generally similar voice consisting of rapidly repeated melancholy hoots that increase and then decrease in acoustic frequency over time.

G. n. hallsi differs (in vocal characters to Levels 1, 4 and 5) from *G. n. nana* of the East Andes by its paler (more orange, less ferruginous) underparts and more olivaceous dorsal plumage; from the northern East Andes population described below in the lower acoustic frequency of its song and call; from *G. n. occidentalis* of the Central Andes by its more olivaceous dorsal plumage and lower acoustic frequency of its song; and from the West Andes population by its more olivaceous dorsal plumage, shorter song length and reduced frequency variation in its song. The new subspecies' song differs in at least three vocal variables from all Venezuelan populations (see Appendix 4), and would merit species rank but for the existence of intermediate populations with fewer diagnosable differences. Other differences between *G. n. hallsi* and *G. nana* populations are presented in Appendix 4.

Description of the holotype.—See Fig. 1. Colours follow Munsell (1977, 2000). Description taken immediately after collection. Lores, central forehead and crown dark grey (Gley 1 3/N). Mantle, upperwing and tail generally brown (2.5Y 3/2), becoming darker and richer brown (less olivaceous: 2.5Y 2.5/1) on folded wing, particularly on primary-coverts and outer webs of flight feathers and rectrices. Large loreal spot, eye-ring, breast, throat, flanks, underwing-coverts, tip of largest alula and tip of outermost primary rufous-orange (7.5YR 5/8 or 5YR 5/8, but more rufous). Lower and central belly white. Feathers of underparts dark grey basally with rufous-orange tips (majority, including flanks and breast), white basally with rufous-orange tips and dark shaft (throat) or dark basally with white tips (lower belly). Blackish streaks below eye and in throat area. Rictal bristles black and 5–7 mm long. Irides dark reddish brown (2.5YR 2.5/3). Legs dark grey (Gley 4/N). Bill mostly dark grey (Gley 2.5/N) with pinkish base to lower mandible. Longest primary p6; small emarginations on pp7–9. Narrow yellowish tips to median and lesser coverts. Ovary sac 5 mm × 2 mm. Skull c.90% ossified. Stomach contents: coleoptera exoskeleton and other insect remains. Measurements (in mm): wing in life: 78.0, wing-chord (skin) 74.0; tail 33.0; tarsus 32.0; bill to skull 15.0 mm; bill depth at nostrils 4.8 mm; bill width at nostrils 5.2 mm.

Variation in the series.—The paratype from Lepipuerto had a smaller ovary sac (<1 mm) and the skull c.70% ossified, and was thus slightly younger, although it had attained adult plumage. It lacked yellowish tips to the median and lesser coverts and had stronger (but still faint) dark throat streaking. The La Aurora bird is similar to other specimens, but had a larger ovary sac, skull c.90% ossified and more extensive white on the lower belly. Variation in biometrics and voice of *G. n. hallsi* are detailed in Appendices 2–3.

Vocalisations.—The song of *G. n. hallsi* is generally similar to that of other taxa, being a rapid series of melancholy, high-pitched hoots (Fig. 10h; Appendix 2). The call is similar to that of other populations (except *G. n. pariae* and *G. n. cumanensis*), being a single downstroke or falling whistle (*siu*) (Figs. 12c–d). A distress call, given in the hand, was a harsh 0.3-second screech (concentrated at 2–6 kHz) after a typical downstroke, *siu-chaaaa*, and is perhaps not given frequently in nature.

Distribution.—Apparently endemic to Serranía de los Yariguíes (Fig. 9), where known from three localities, two on the west slope (2,450–2,900 m) and one on the east (2,750 m). At one site, it was recorded immediately below the treeline. Such habitat occurs to 3,200 m on the east slope of Serranía de los Yariguíes (*cf.*, in the west Andes, records up to 3,300 m: Krabbe *et al.* 2006). *G. n. nana* and *G. n. occidentalis* likewise generally occur only in high-elevation humid forest. Records of *G. nana* in Colombia below c.2,000 m (e.g. Hilty & Brown 1986) probably reflect either inaccurate locality data or the lower elevations at which some Venezuelan taxa are found. *G. ferruginepectus* / *rara*, *G. cucullata* and *G. flavirostris* generally replace *G. nana* below 2,000–2,400 m in appropriate habitat in Colombia.

Habitat and ecology.—Found only in high-elevation montane cloud forest characterised by a broken canopy, many epiphytes, abundant tree ferns, bamboo and other successional plant species. A number of treefalls occurred during field work at study sites where *G. nana* was recorded. The families Moraceae (*Ficus*), Clusiaceae, Poaceae (*Chusquea*) and Actinidaceae (*Saurauia*) are present in this habitat. *G. nana* frequently uses *Chusquea* for nesting (Greeney *et al.* 2008). Rainfall and humidity is considerably higher in Serranía de los Yariguíes than elsewhere in the East Andes (Donegan & Avendaño 2008).

In January at the type locality and in November at Alto Cantagallos, *G. n. nana* was heard singing daily in the two hours after dawn (05.30–07.30 h). It was not heard at La Aurora in July 2005 or April 2006. Singing in November–January might be indicative of the onset of breeding, as many birds nest in the middle Magdalena Valley region in March–April (Cuervo *et al.* 2001). All Yariguíes captures were in mid–late morning and immediately prior to the onset of thunderstorms.

History.—*G. n. hallsi* was initially found and collected during an expedition to the highest elevations of Serranía de los Yariguíes in January 2005. Personnel comprised TMD, B. Huertas J. J. Arias, M. Donegan and J. Pinto. Two females were collected and sound-recordings were made. Details of the expedition and other ornithological results appear in Donegan & Huertas (2005) and Donegan *et al.* (2007). A third specimen was obtained in July 2005 at another high-elevation site in Yariguíes (Huertas & Donegan 2006) and J. E. Avendaño-C. confirmed the presence of *G. n. hallsi* at a third site in Serranía de los Yariguíes in 2006 (Donegan *et al.* 2007). This is the fourth new taxon to be described as a result of our work (Donegan & Huertas 2006, Huertas & Arias 2007, Donegan & Avendaño 2008).

Etymology.—The subspecies epithet honours the late Alan G. Halls of Caversham, UK (d. January 2005, simultaneous with the discovery of *G. n. hallsi*). Alan's surname is formed as a fictional second declension Latin noun *Hallsus* and declined in the genitive singular. Alan became a keen birder in the 1950s and his enthusiasm for birds and tutoring younger people, including myself, never waned. He authored monthly bird articles in his local newspaper, *Caversham Bridge*, for many years. Alan was a modest person and may have balked at the notion of a bird named in his honour, but this discovery and others owe much to his encouragement. The name *hallsi* is not known to be preoccupied or used for any other Grallariidae.

Discussion.—The reasons for the presence of multiple distinctive subspecies in the East Andes are enigmatic (Donegan *et al.* 2007). *G. n. hallsi* is intriguingly closer to *G. n. nana* in, for instance, acoustic frequency of song, song length and number of notes, but closer to the new taxon described below in, e.g., plumage, song speed and change of pace in the song. The shortest and highest-elevation 'bridge' between Yariguíes and the main East Andes is closer to the range of *G. n. nana*. A not dissimilar pattern occurs in *Scytalopus griseicollis*, with *S. g. gilesi* endemic to Yariguíes and two other subspecies in the main East Andes with a north–south divide. Similar upperparts plumage in Yariguíes and Tamá may reflect convergent evolution, as Gloger's Rule (Zink & Remsen 1986) determines that plumage is darker in more humid regions (or here, more olivaceous and less brown dorsal plumage).

A new subspecies from the Venezuelan Andes

Hellmayr (1917) noted morphological differences between specimens from the Mérida range and 'Bogotá', and presented biometric data for the two populations. However, he provisionally included the Venezuelan population within *G. n. nana* given the lack of reli-

able locality data for the Bogotá specimens and the paler plumage of one of them. I suspect that the paler bird was of *G. n. occidentalis*, as this taxon is also represented by 'Bogotá' specimens at BMNH and AMNH.

Hellmayr (1917) further commented: 'The two Bogotá specimens are remarkably dark, the third however is quite consistent with the Mérida series, which by the way to some extent varies in the colouring of the underparts and upperparts. Provisionally, I might have combined therefore the Colombian and west Venezuelan regions' birds, particularly since the so-called Bogotá skin delivers no adequate study objects anyhow.' Subsequently, Cory & Hellmayr (1924) noted that 'Birds from the Andes of Mérida agree with one from 'Bogotá', while two other 'Bogotá' skins are conspicuously darker, both above and below. A good series of fresh specimens from the type locality should be compared.' These remarks appear to have been subsequently forgotten, although K. C. Parkes also considered the Mérida population to represent an undescribed subspecies (handwritten notes at AMNH).

Given the availability now of reliable locality, morphological and vocal data for *G. nana* populations in the East Andes, it is possible, at last, to confirm Hellmayr's suspicion that birds from Mérida merit taxonomic recognition. Those on the other side of the Táchira depression, in Tamá National Park and environs, show statistically significant differences in song length, number of notes, song speed and acoustic frequency from Mérida birds. However, none of these differences reaches Level 2 or more. Their plumage is also similar. The Tamá population is therefore, provisionally, treated within the following new subspecies of *G. nana* in the Venezuelan Andes (and northern East Andes).

Grallaricula nana nanitaea subsp. nov.

Holotype.—American Museum of Natural History, New York, USA (AMNH 146661). Adult male collected by Briceño, S. B. Gabaldón and sons at La Culata, near Mérida, Venezuela, at an elevation of 3,000 m, on 24 January 1911. This locality is at c.08°45'N, 71°05'W (Paynter 1982).

Paratypes.—All were collected at the same locality as the holotype. AMNH 96305 is an adult male collected by S. B. Gabaldón at 2,000 m on 28 May 1904. AMNH 492317 is an adult male collected by Briceño (no other data). Other specimens pertaining to this taxon but not designated as types are listed in Appendix 2 and come from the range formerly assigned to *G. n. nana* in Venezuela, *per* Hilty (2003) and Restall *et al.* (2006). Specimens from the Tamá region and Suratá, dpto. Santander, are also provisionally assigned to this subspecies, but are not designated as types.

Diagnosis.—Referred to the *G. nana* group by the same rationale as for *G. n. hallsi*. Differs (in vocal characters to Levels 1, 4 and 5) from *G. n. hallsi* in its higher frequency song (and, in the case of the Mérida population alone, also higher frequency call, faster song with greater acoustic frequency variation and greater number of notes). From *G. n. nana*, it can be separated by its more olivaceous back, paler breast and higher acoustic frequency in its song and calls. From *G. n. occidentalis* and the West Andes population it differs in its more olivaceous mantle, and from *G. n. olivascens* in its less olivaceous mantle and slower song. Other differences between *G. n. hallsi* and other *G. nana* populations are presented in Appendix 4.

Description of the holotype.—Lores, central forehead and crown dark grey (Gley 1 3/N). Mantle and tail generally brown (10YR 3/3), becoming richer brown (less olive) over upperwing, particularly on the primary-coverts and outer webs of the flight feathers and

rectrices. Large loreal spot, eye-ring, throat, breast, flanks, underwing-coverts, tip of largest alula and tip of outermost primary orange-rufous (7.5YR 5/8 or 5YR 5/8 but more rufous). Central belly white. Small and indistinct patch of feathering on upper breast white. Breast feathers dark grey basally with rufous tips (most of flanks and breast), white basally with rufous tips (throat) or dark basally with white tips (white of breast and lower belly). Trailing edge of primaries pale grey distally. Rictal bristles black and 5–7 mm long. The specimen's label states that the irides are blue, as implausibly noted for various other *G. nana* collected by Briceño and Galbadón. This population has a dark brown iris. Measurements (mm): Wing chord 66.0; tail 31.0; tarsus 31.0; bill to skull 16.5; bill width at nostrils 4.0.

Variation in the series.—Biometric and vocal data (including vocal differences between the Tamá and Mérida populations) are presented in Appendices 2–3. Depictions of *G. n. nanitaea* appear in Hilty (2003) and Restall *et al.* (2006), both labelled *G. n. nana*. Fig. 7 shows the AMNH Mérida series. There is notable variation in the extent of the white breast collar. Photographs of live birds suggest that this is invisible in life, but it may be visible in singing males, and appears reduced in female specimens. Juveniles COP 73942 and 14524 both have asymmetrical patches of dark rufous (2.5YR 3/4) feathering on the rear crown and breast, and stronger blackish markings on the throat and chin (Restall *et al.* 2006), but typical upperparts (see Fig. 2). Asymmetric dark rufous patches are also a feature of juvenile *G. n. occidentalis* (e.g. AMNH 184358), the West Andes population (ICN 25921) and *G. n. olivascens* (Phelps & Phelps 1949, Restall *et al.* 2006), but unknown in *G. n. pariae* or *G. n. cumanensis*. COP 62203–04 possess a less extensive pale bill base.

Distribution.—Known from the entire Mérida range of the Andes in Venezuela, at least from north-east Trujillo to Táchira, but replaced in the Coastal Cordillera of Venezuela by *G. n. olivascens* (Fig. 9a). In the East Andes, the potential ranges of *G. n. nanitaea* and *G. n. nana* are separated by a habitat discontinuity associated with the río Chicamocha Valley (Fig. 9b). Other high-elevation birds showing geographical variation in this region (e.g. *Chlorospingus ophthalmicus*, *Atlapetes schistaceus*, *Scytalopus griseicollis*) may have similar subspecies distributions.

Ecology.—Colombian Tamá specimens were collected in high-elevation cloud forest with a dense understorey dominated by *Rhipidocladium* sp. (label data).

Etymology.—The subspecies epithet is a non-variable combination of two Spanish-language words, suggestive of a diminutive version of the subspecies name presently assigned to this population, *nana*. The full name *Grallaricula nana nanitaea* recalls the Spanish advent carol 'A la nanita nana nanita ea'. The name *nanitea* is not known to be preoccupied or used for any other Grallariidae.

Is *G. n. pariae* a valid subspecies?

G. n. cumanensis occurs in the Caripe Mountains (type locality Las Palmares and Rincón San Antonio, Cumaná, c.10°17'N, 63°45'W: Paynter 1982) in the eastern mainland of Sucre state, Venezuela (Hartert, 1900, 1922). *G. n. pariae* is considered endemic to the Paria Peninsula, with the type locality at Cerro Azul, Sucre, Venezuela (c.10°40'N, 61°56'W: Paynter 1982).

G. n. pariae was described as differing from *G. n. cumanensis* in its darker upperparts and more olivaceous back with a less yellowish tinge (Phelps & Phelps 1949). Such differences may have been apparent on fresh specimens, but no diagnostic plumage differences

were noted during this study, thereby calling into question the validity of *G. n. pariae*. Nonetheless, songs were statistically significantly different in maximum acoustic frequency (Level 1), whilst *G. n. cumanensis* has a narrower bill (Levels 1 and 2) and individual trills showed apparent Level 5 differences in song speed, although this is based on a single recording of *G. n. cumanensis*. Trill speed is thought to be constrained by the size and mass of the bill (Podos *et al.* 2004). The faster trill and narrower bill of *G. n. cumanensis* could therefore result from the same adaptation. As *G. n. cumanensis* meets at least some subspecies concepts, synonymy is not proposed.

Species limits

Treatment of *G. nana* as a single species does not accord with any species concept in modern use. All described taxa, except perhaps *G. n. occidentalis* and *G. n. pariae*, are phylogenetic species (*per* Cracraft 1983), whilst *G. n. cumanensis* / *pariae* and *G. n. kukenamensis* emerge as candidates for species rank under a modern interpretation of the Biological Species Concept (Helbig *et al.* 2002).

In the Andean and Coastal Cordillera subspecies *nana*, *occidentalis*, *hallsi*, *nanitaea* and *olivascens* (hereafter '*nana* group'), inter-population plumage and biometric differences are relatively small. Up to Level 5 differences, in at most a single vocal variable, were observed between geographically adjacent populations. That parapatric or sympatric *Grallaricula* species studied all show diagnosability in three or more vocal characters does not mean that populations with fewer diagnosable vocal differences would fail to interbreed. However, in light of recently reported inter-species hybridisation between two sympatric Grallariidae (Cadena *et al.* 2007), a cautious approach is adopted. It is doubtful whether small or overlapping vocal differences, such as those among adjacent populations in the *nana* group, would pose a barrier to reproduction in the hypothetical event of their being found together. Subspecies rank is therefore a plausible treatment under the Biological Species Concept for the *nana* group.

The modest differences between members of the *nana* group contrasts with the substantial shift in biometric, plumage and vocal characters between allopatric *G. n. olivascens* of the Coastal Cordillera and *G. n. cumanensis* of the Caripe Mountains (Figs. 3, 8, 11 and 12). *G. n. cumanensis* and *G. n. pariae* (hereafter '*cumanensis* group') are diagnosably different from all other *G. nana* populations in their darker and more rufous underparts coloration, more extensively white belly, presence of a more elongated orange loreal mark, presence of a white postocular spot; broader based, thicker, less tapering and more extensively pale bill; faster, lower frequency song with more staccato note shape; and strikingly different trilling call. Both members of the *cumanensis* group differ from all populations and subspecies in the *nana* group in at least three variables to their song. Vocal differences between the *cumanensis* and *nana* groups are therefore equivalent to those between sympatric *Grallaricula* species. Moreover, the geographically closest race (*G. n. olivascens*) differs even more radically from the *cumanensis* group than some more distant populations of the *nana* group, exhibiting diagnosable differences in four variables to its song, as well as in tail length, tarsus length, bill width and bill shape (Appendix 4). The combination of vocal, biometric and plumage differences mandate species rank for the *cumanensis* group with respect to the *nana* group.

Drawing species limits in *G. nana* is complicated by the lack of vocal data for morphologically diagnosable *G. n. kukenamensis* of the tepuis. This is geographically the most isolated taxon, being separated by at least 350 km of unsuitable lowland habitat from other populations. By contrast, the *nana* and *cumanensis* groups are separated by 200 km (Fig. 9). *G. n. kukenamensis* occurs in mountains that are considered to predate the Andes and where

'basal' taxa are sometimes revealed in molecular studies (Rheindt *et al.* 2008). It is diagnosable from all members of the *nana* group by its shorter tarsus (Level 5), and from geographically proximate *olivascens* and *nanitaea* in its broader bill and shorter tail. It is closer to the *nana* group than *cumanensis* group in overall plumage, but differs in plumage saturation of both upperparts and underparts (Fig. 4). The described single-note call (Braun *et al.* 2003; Fig. 12m), if confirmed, would be similar in length and acoustic frequency to calls of the *nana* group but could not be confused with *cumanensis* group calls. *G. n. kukenamensis* is not diagnosable from the *cumanensis* group in biometrics, other than bill shape (Fig. 8), but shares all plumage differences from these taxa with the *nana* group (described above). The tentative recording of the song of *G. n. kukenamensis* differs (to Levels 4/5) from that of all other *G. nana* taxa in note shape, song length and number of notes, and compared to the *cumanensis* group, the song differs in note shape, length, number of notes, speed and acoustic frequency. In each case, more than three differences were observed (the benchmark for species rank). Although the statistical tests employed are highly conservative, they are based on a single recording only tentatively identified and make assumptions about variance of vocal variables in the *G. n. kukenamensis* population.

Four possible approaches to species limits must be considered under a modern interpretation of the Biological Species Concept (Helbig *et al.* 2002): (i) split the *cumanensis* group and lump *kukenamensis* within the *nana* group; (ii) split the *cumanensis* group and lump *kukenamensis* within the *cumanensis* group; (iii) treat the *nana* group, *cumanensis* group and *kukenamensis* as three species; and (iv) retain *G. nana* as a single species. The first approach would be supported by differences in plumage and calls, but is inconsistent with biometrics. Lumping *kukenamensis* within the *cumanensis* group would be supported by biometrics (tarsus length and bill width), but inconsistent with plumage, bill morphology and calls. Retention of *G. nana* as a single species is precluded because the *nana* and *cumanensis* groups exhibit vocal differences equivalent to those between sympatric *Grallaricula* species. A three-way split is therefore the better approach under a modern Biological Species Concept. Given that several other phylogenetic species are involved, this split is conservative. However, I recognise that taxonomists who prefer a 'status quo is best' approach (e.g. some contributors to Remsen *et al.* 2008) will probably prefer to wait for definitive vocal data for *G. n. kukenamensis* or a molecular study before changing current treatments.

Ridgely & Tudor (1994) proposed Paria Antpitta as a vernacular name for *G. n. cumanensis*. However, the species-group to which it belongs is not restricted to the Paria Peninsula and would not take the name *pariae*, which is junior to *cumanensis*. I suggest Sucre Antpitta as a more appropriate name for the *cumanensis* group given that it is near endemic to that state, extending only marginally into north Monagas and north-east Anzoátegui. Guianan Antpitta could be used for *G. n. kukenamensis* (Tepui Antpitta is already used for *Myrmothera simplex*). Given that the Andean and Coastal Cordillera species *G. nana* is so widespread, it should retain the English name Slate-crowned Antpitta, even if split.

Conservation

The *cumanensis* group is probably threatened. It is locally common but few modern-day localities are known. The two species endemic to the Paria Peninsula and Caripe Mountains with a similar range to the *cumanensis* group, White-throated Barbtail *Premnoplex tatei* and Venezuelan Flowerpiercer *Diglossa venezuelensis*, are both treated as threatened. Various other endemic birds with smaller distributions within the Caripe-Paria region Endemic Bird Area are also threatened (Stattersfield *et al.* 1998). *G. cumanensis* is probably Endangered, given its similar habitat use and elevational range to *P. tatei*. *G. n. kukenamensis* and the *nana*

group should be regarded as Least Concern on the basis of their range sizes compared to species of similar distribution.

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APPENDIX 1: Materials examined

Specimens

- G. n. occidentalis* ECUADOR: AMNH 184353–55, 184358 (juvenile), 186377 (Sumaco, Napo); MNHN unnumbered (Choconta). WEST ANDES, COLOMBIA: ANSP 142395 (photograph) (Gamboia = San Antonio, Cauca, 02°37'N, 76°54'W, 2,012 m); IAVH 13387, 13410 (Parque Nacional Natural Tatamá, Risaralda, 05°12'N, 76°06'W); ICN 25920–21 (Corea, Farallones de Cali, Valle, 03°22'N, 76°53'W, 2,700 m); LACM 30858–59 (Cerro Munchique, El Tambo, Cauca, 02°32'N, 76°57'W, 2,500 m). *Not examined*: ANSP 142394, 144677 (El Tambo, Cauca, 02°25'N, 76°49'W, 1,829 m); FMNH 249745–46 (Cerro Munchique, as above); Museum of Natural History, Geneva (MHNG) 1128.022 (Cerro Munchique, as previous, 2,000 m); NMNH 446635 (Cerro Munchique, as previous); Peabody Museum of Natural History (PMNH) 54539 (Cerro Munchique, as previous, 2,200 m). *Note*: AMNH 108099 (San Antonio, La Cumbre, Valle del Cauca, 03°30'N, 76°38'W, 1,800 m) is *G. flavirostris*. CENTRAL ANDES, COLOMBIA: AMNH 112010 (above Salento, Quindío, 04°38'N, 75°34'W, 3,000 m), 112011 (Laguneta, Quindío, 04°35'N, 75°30'W, 3,090 m), 492309 ('Bogotá'); ANSP 155176 (photograph) (Laguneta, as above, 2,134 m); BMNH 89.9.10.928 ('Bogotá'), 89.9.10.929 (Medellín, 06°15'N, 75°35'W), 89.9.10.930 (Santa Elena, Medellín, 06°15'N, 75°34'W); CM 70299, 70423, 70434 (holotype; photograph) (El Zancudo, Manizales, Caldas, 05°05'N, 75°30'W); IAVH 13072–73 (Parque Municipal Campoalegre, Risaralda, 04°52'N, 75°31'W, 2,470 m); MNHN 653 ('Antioquia'). *Not examined*: Nationaal Natuurhistorisch Museum, Leiden (RMNH) g.n.0.1 (Medellín, Antioquia, 06°15'N, 75°35'W); National Museum of Natural History, Washington DC (NMNH) 436475–76 (Sonsón, Antioquia, 05°42'N, 75°17'W); Museo de Historia Natural, Universidad del Valle, Cali (MHNLUV) 4731 (no locality), 4802–04 (Salento, Quindío, 04°38'N, 75°34'W, 2,140 m), 6165 (Ucumari, Santa Rosa de Cabal, Risaralda, 04°46'N, 75°37'W, 2,400 m).
- G. n. subsp.?* HEAD OF MAGDALENA VALLEY, COLOMBIA: ANSP 155852 (photograph) (San Agustín, Huila, 01°50'N, 76°20'W); IAVH 2489 (Quebradón, Moscopán, Cauca, 02°14'N, 76°10'W, 2,285 m). *Not examined*: MHNLUV unnumbered (Moscopán, La Plata, Huila/Cauca, 02°20'N, 76°05'W, 2,300 m); FMNH (photograph) 292120–25 (Llorente, Tumaco, Nariño, 00°49'N, 77°15'W), 292119 (La Victoria, Ipiales, Nariño, 00°35'N, 77°10'W); MNHG 1179.045 (as previous, 2,800 m).
- G. n. nana* EAST ANDES, COLOMBIA: BMNH 44.12.31.21, 54.1.25.81 ('New Grenada'), 89.9.20.651–652, 89.9.10.929 ('Bogotá'); ICN 31322 (Capenta, Junín, Cundinamarca, 04°34'N, 73°41'W, 2,600 m); MCZ 76739 (holotype; photograph) ('Colombie'). *Not examined* (presumably this or *G. n. occidentalis*): MCZ 30816 ('Bogotá'). PICACHOS, COLOMBIA: IAVH 10253–55 (Parque Nacional Natural Los Picachos, Finca Andalucia, Caquetá, 02°44'N, 74°53'W, 2,000 m).
- G. n. hallsi* (for details see text): ICN 35195 (holotype), 35193 (paratype), 35555 (paratype).
- G. n. nanitaea* MÉRIDA, VENEZUELA: AMNH 96305 (Culata, Mérida, 08°45'N, 71°05'W, 2,000 m), 100209, 492311–13 (Walle [=Valle], 08°70'N, 71°06'W, 2,165 m), 146661 (holotype, Culata, 3,000 m), 492317 (paratype, Culata), 492314–16 (El Escorial, Mérida, 08°38'N, 71°05'W), 492318 (Mérida); COP 4958 (Páramo Misisí, Trujillo, 09°20'N, 70°20'W, 2,100 m), 14524 (Quintero, Mérida, 2,500 m), 19961–62 (Páramo Cendé, Trujillo, 08°40'N, 71°00'W, 2,700 m), 24544–46 (Boca de Monte, Pregonero, Táchira, 08°01'N, 71°46'W, 2,400 m), 65392 (La Azulita, Mérida, 08°43'N, 71°27'W, 2,300 m); MNHN 652 (Mérida). SANTANDER–TAMÁ: VENEZUELA: COP 73941–43 (Cumbres Cerro Retiro, Revancha, Táchira, 07°30'N, 72°23'W, 2,800 m), 74419–20 (Copas La Revancha, Táchira, 07°30'N, 72°23'W, 2,800 m), 62203–06 (Hacienda La Providencia, Río Chiquito, Táchira, 07°19'N, 71°37'W, 2,100–2,300 m). COLOMBIA: IAVH 10702, 10714, 10722 (Parque Nacional Natural Tamá, Herrán, Norte de Santander, 07°26'N, 72°27'W, 2,430 m); ICN 33933 (as IAVH specimens), 36125 (Vereda El Monsalve, Suratá, Santander, 07°23'N, 73°00'W, 3,000 m). *Not examined*: FMNH 43602 (Páramo de Tamá, Norte de Santander, 07°25'N, 72°26'W).
- G. n. olivascens* COASTAL CORDILLERA, VENEZUELA: AMNH 155733 (no locality), 322978 (Colonia Tovar, 10°25'N, 67°17'W, 1,900 m), 492319 (Galipán, Cerro del Avila, north of Caracas, 10°32'N, 66°53'W, 2,000 m); BMNH 1915.3.16.8–16.9 (Galipán, Caracas, 10°34'N, 66°54'W); COP 1467–68, 3444 (Colonia Tovar, 1,800–1,950 m), 13052, 50090, 56779 (Junquito, Distrito Federal, 10°28'N, 67°05'W, 2,000 m), 58453–54 (locality not noted), 61638–41 (Junquito, Distrito Federal), 62590 (Estación Teleférico, Cerro El Avila, 2,100 m), 62591, 62593–94 (Galipán, 1,900 m), 75776 (Fundo Jeremba, Colonia Tovar).
- G. n. cumanensis* CARIBE, VENEZUELA: AMNH 188255 (La Latal, Sucre, 10°10'N, 63°55'W, 1,000 m), 492322 (Río San Antonio, Cumaná, 10°27'N, 63°50'W), 492321 (paralectotype, Los Palmales, Cumaná); COP 15537 (Cerro El Pecnió, Bergantín, Anzoátegui, 10°01'N, 64°22'W, 1,300 m), 23057 (Cerro Negro, Caripe, Monagas, 10°12'N, 63°29'W, 1,500 m).
- G. n. pariae* PARIÁ, VENEZUELA: AMNH 388107 (paratype) (Cerro Humo, Irapa, Sucre, 10°40'N, 62°30'W, 1,100 m); BMNH 1957.1.2 (paratype, Maino, Cerro Humo, Sucre); COP 40514–22 (paratypes) (La Cumbre, Cerro Azul, Sucre, 10°40'N, 61°56'W, 820–920 m), 41051–56 (paratypes) (Cerro Humo, Irapa, Sucre, 1,000 m), 44012–30 (paratypes) (Cerro Azul, Sucre, 900–920 m), 44240–54 and 44256–58 (paratypes) (Cerro Humo, Sucre, 1,000–1,200 m), 57002–12 (Cerro Humo, Irapa, Sucre, 920 m).

- G. n. kukenamensis* TEPUIS, GUYANA?: BMNH 89.7.10.926 (holotype) (Mt. Kukenam, 1,500 m). VENEZUELA: AMNH 236691–92 (Mt. Roraima, 05°09'N, 60°47'W, 2,000 m); COP 4240 (Arabupu, Mt. Roraima, 05°06'N, 60°44'W), 24956, 27095–99 (Ptari-tepui, Bolívar, 05°46'N, 61°46'W, 1,300–1,900 m), 27087–94, (Sororopán-tepui, Bolívar, 05°45'N, 61°43'W, 1,400–1,800 m), 35779–81 (Chimantá-tepui, Bolívar, 05°18'N, 62°10'W, 700–1,850 m), 42094–95 (Acopán-tepui, Bolívar, 05°12'N, 62°14'W, 1,800 m), 79001 (km 125 on El Dorado–Santa Elena road, Bolívar, c.05°28'N, 61°00'W, 1,350 m).
- G. f. ferruginepectus* VENEZUELA: BMNH 1915.3.16.4, 1915.3.16.7 (Galipán, Caracas); COP 18518–19, 18521–23, 18525–26, 71734, 72054, 72056 (details not noted). COLOMBIA: IAVH 10921 (Parque Nacional Natural Tamá, Norte de Santander, 07°06'N 72°14'W, 1,250 m); MLS 3946 (El Diamante, Norte de Santander).
- G. f. rara* VENEZUELA: BMNH 1952.39.1 (Cerro Pejochaina, Caracas); COP 54875–76, 54880, 54921–25, 57608, 72837 (details not noted). COLOMBIA: MLS 3944–45 (La Victoria, Sasaima, Cundinamarca); MNHN 2001.656 ('Colombia').
- G. f. subsp.* COLOMBIA: IAVH 11953–54, 11997–98, 12001, 12007 (Río Tapias, Hacienda Tintina, Neira, Caldas, 05°14'N, 75°41'W, 1,080 m).
- G. cucullata* COLOMBIA: NHM 89.9.10.932, 89.9.20.59 (Santa Elena, Antioquia), 89.9.20.655 ('Bogotá').

Sound-recordings

XC = www.xeno-canto.org catalogue numbers; IAVH = Instituto Alexander von Humboldt sound archive numbers; and Cornell to Cornell Lab of Ornithology archive numbers.

- G. n. occidentalis* PERU: Cordillera del Cóndor, Cajamarca (04°54'S, 78°54'W, 2,300 m) (T. Mark: XC 7013); Cerro Chinguela, Cajamarca (05°07'S, 79°25'W) (T. A. Parker *in* Isler & Whitney 2002); Montana Negra, Cordillera del Cóndor, Cajamarca (05°04'S, 78°44'W, 2,450 m) (T. Mark: XC 10434); Paja Blanca, Cajamarca (06°24'S, 79°07'W, 2,900 m) (F. A. Pratonlongo); Bosque de Protección Pagaibamba (06°26'S, 79°04'W, 3,000 m) (F. A. Pratonlongo). ECUADOR: Guacamayos, Napo (00°37'S, 77°50'W, 2,000–2,200 m) (W. Halfwerk: XC 10602–03; R. Ahlman: XC 13225; Krabbe *et al.* 2001, Krabbe & Nilsson 2003); Volcán Corazón, Zamora-Chinchipec (Krabbe *et al.* 2001); Cabañas San Isidro, Napo (00°35'S, 77°53'W, 2,100 m) (N. Athanas: XC 5060; Moore & Lysinger 1997); Arenales, Río Paute, Azuay (02°34'S, 78°34'W, 2,350–2,400 m) (Krabbe & Nilsson 2003); km 5 on Santa Barbara–La Bonita road, Sucumbíos (00°39'N, 77°30'W, 2,700 m) (Krabbe & Nilsson 2003); Tapichalaca Biological Reserve, Zamora-Chinchipec (04°29'S, 79°07'W) (B. Harris). WEST ANDES, COLOMBIA: Páramo Frontino, Antioquia (06°26'N, 76°05'W, 3,100–3,200 m) (N. Krabbe); Pueblo Rico, Risaralda (05°09'N, 76°02'W, 2,620–2,680 m) (S. Córdoba: IAVH 15968, 15972–76). CENTRAL ANDES, COLOMBIA: Río Blanco, Caldas (05°04'N, 75°32'W, 2,400–2,500 m) (D. Calderón: XC 'mysteries' page, 300, 306; B. Davis: XC 13907, 17622; H. van Oosten: XC 18290; M. Álvarez: IAVH 11452, 11479); El Guayabo, Neira, Caldas (05°14'N, 75°03'W, 3,600 m) (Álvarez & Córdoba 2002, Álvarez *et al.* 2007: IAVH 7406, IAVH 7401–08 [treated as same recording], IAVH 7736, 7791, 10055); Alto de San Sebastian–La Castellana, Antioquia (06°03'N, 75°35'W, 2,700 m) (A. M. Cuervo); Finca Los Molinos, Ibagué, Tolima (04°26'N, 75°14'W, 2,000–2,200 m) (O. Laverde: XC 12421; IAVH 17268); Reserva Natural Ibanasca, Ibagué (04°35'N, 75°14'W, 2,300–2,600 m) (O. Laverde); Parque Municipal Campoalegre, Finca La Granja, Risaralda (04°52'N, 75°31'W, 2,470–2,680 m) (S. Córdoba: IAVH 15266). HEAD OF MAGDALENA VALLEY, COLOMBIA: Reserva Los Yalcones, San Agustín, Huila (01°47'N, 76°21'W, 2,420–2,600 m) (D. Calderón: IAVH 16521, 16523, 16552).
- G. n. nana* EAST ANDES, COLOMBIA: Rogitama, Arcabuco, Boyacá (05°47'N, 73°31'W, 2,500 m) (J. Zuluaga); Cañon del Río Pómecca, Arcabuco, Boyacá (05°48'N, 73°28'W, 2,600 m) (Álvarez 2000: IAVH 10442; also IAVH 10437, 10439–40); Finca San Cayetano, Bojacá, Cundinamarca (04°37'N, 74°18'W, 2,650 m) (O. Laverde); Reserva Forestal Río Blanco, La Calera, Cundinamarca (04°42'N, 73°51'W, 3,000 m) (F. G. Stiles: IAVH 10848). PICACHOS: Parque Nacional Natural Pichachos–Río Pato, San Vicente del Caguán, Caquetá (02°48'N, 74°51'W, 1,300–2,000 m) (M. Álvarez: IAVH 345).
- G. n. hallsi*: Serranía de los Yariguíes (details above) (T. M. Donegan).
- G. n. nanitaea* MÉRIDA, VENEZUELA: La Carbonera, Mérida (08°38'N, 71°22'W, 2,300 m) (P. Schwarz: Cornell 62191); Páramo Zumbador, Táchira (08°00'N, 72°05'W, 2,450–2,800 m) (P. Schwarz: Cornell 62189–90, 62192–93); Parque Nacional Sierra Nevada, Mérida (08°37'N, 17°02'W, 2,400 m) (N. Athanas: XC 6858; A. Spencer: XC 9895; B. M. Whitney); Universidad de Los Andes, Mérida (K. J. Zimmer); La Azulita, Mérida (08°43'N, 71°27'W) (R. Behrstock); El Morro–Aricagua road, Mérida (08°17'N, 71°09'W) (Boesman 2007); Parque Nacional Guaramacal, Trujillo (09°10'N, 70°11'W, 1,600–3,000 m) (Boesman 2007). SANTANDER–TAMÁ, COLOMBIA: Sisavita, Cucutilla, Norte de Santander (07°28'N, 72°51'W, 2,400 m) (S. Córdoba: IAVH 8660, 8662, 8813); Parque Nacional Tamá, Herrán, Norte de Santander (07°26'N, 72°27'W, 2,430 m) (M. Álvarez *in* Córdoba & Álvarez 2003, Álvarez *et al.* 2007: IAVH 11722, 11727).

- G. n. olivascens* COASTAL CORDILLERA, VENEZUELA: Colonia Tovar, Aragua (10°25'N, 67°17'W, 1,800–2,200 m) (P. Schwarz: Cornell 62187–88; Boesman 1999; B. M. Whitney; M. Isler; P. Coopmans).
- G. n. cumanensis* CARIBE, VENEZUELA: Cerro Negro, Monagas (10°14'N, 63°34'W, 1,200–1,700 m) (Boesman 2007); Piedra de Moler, Sucre (10°06'N, 63°49'W, 1,840 m) (C. A. Marantz).
- G. n. pariae* PARIA, VENEZUELA: Paria Peninsula, Sucre (10°41'N, 62°37'W, 600–1,000 m) (Boesman 1999); Cerro Humo, Sucre (10°40'N, 62°30'W, 700 m) (R. Innes; J. I. Areta), as previous (10°42'N, 62°37'W, 950 m) (N. Athanas: XC 3533).
- G. n. kukenamensis* TEPUI, VENEZUELA: (80% certain, as bird unseen) Upper Escalera, Bolívar (05°58'N, 61°24'W) (P. Boesman).
- G. lineifrons* ECUADOR: (all Krabbe & Nilsson 2003, unless stated): Cerro Mongus, Carchí (00°27'N, 77°52'W, 3,300 m); 3–5 km below Oyacachi, Napo (00°13'S, 78°02'W, 3,300 m); Acanamá, Loja (03°41'S, 79°15'W, 3,100 m); Páramos de Matanga, Morona-Santiago (03°18'S, 78°53'W, 3,000–3,250 m); Saraguro, Loja (03°36'S, 79°13'W) (A. Spencer: XC 17214–15).
- G. f. ferrugineipectus* VENEZUELA: Serranía de San Luis, Falcón (11°12'N, 69°42'W, 1,000–1,600 m) (Boesman 1999); Turgua, Aragua (10°25'N, 66°48'W, 800–1,100 m) (Boesman 1999); San Isidro, Barinas (08°50'N, 70°35'W, 1,500 m) (N. Athanas: XC 6857); Caracas, Aragua (P. Schwarz *in* Isler & Whitney 2002).
- G. cucullata* COLOMBIA: La Esmeralda–Río Yurayaco, San José del Fragua, Caquetá (01°21'N, 76° 06'W) (M. Álvarez: IAVH 4260, 4355–56).

Photographs

- G. n. occidentalis* ECUADOR: Cordillera Sabanilla, Zamora-Chinchipe (03°58'S, 79°03'W) (Krabbe & Schulenberg 2003). WEST ANDES, COLOMBIA: Reserva Natural de Aves (RNA) Mirabilis-Swarovski, Cauca (02°31'N, 76°59'W, 2,200 m) (A. Quevedo). RNA Loro Orejiamarillo, Jardín, Antioquia (05°35'N, 75°44'W, 2,400–2,850 m) (J. A. Tobias & A. Quevedo). CENTRAL ANDES, COLOMBIA: RNA Loro Coroniazul y El Mirador, Genova, Quindío (04°08'N, 75°44'W, 3,200 m) (A. Quevedo).
- G. n. nanitaea* MÉRIDA, VENEZUELA: Parque Nacional Guaramacal, Trujillo (09°10'N, 70°11'W) (K. Perez / J. León; Krabbe & Schulenberg 2003). SANTANDER–TAMÁ, COLOMBIA: El Monsalve, Suratá, Santander (07°23'N, 73°00'W, 3,000 m) (J. E. Avendaño: Fig. 2).
- G. n. pariae* PARIA, VENEZUELA: Cerro Humo, details above (J. A. Tobias: Fig. 3).

Biometrics

- G. n. occidentalis* WEST ANDES, COLOMBIA: RNA Mirabilis-Swarovski (details above) (J. P. López *et al.* / ProAves); RNA Loro Orejiamarillo (details above) (G. A. Suárez *et al.* / ProAves); RNA Colibrí de Sol, Páramo Frontino, Antioquia (06°26'N, 76°05'W, 3,400 m) (D. Carantón / ProAves). CENTRAL ANDES, COLOMBIA: Reservas de Aves Comunitarias, Roncesvalles, Tolima (04°00'N, 75°40'W) (A. Bermúdez / ProAves). RNA Loro Coroniazul y El Mirador (details above) (D. Y. Ramírez & D. Osorno / ProAves).
- G. cucullata* COLOMBIA: Nabú, Serranía de los Churumbelos, Cauca (01°36'N, 76°16'W, 1,900 m) (T. M. Donegan, P. G. W. Salaman & A. M. Cuervo).

Other records

- G. n. occidentalis* ECUADOR: Cajanuma, Parque Nacional Podocarpus (04°16'S, 79°00'W) (Ridgely & Greenfield 2001); Reserva Ecológica Cayambe-Coca, Napo (77°50'W, 00°01'S) (Krabbe & Schulenberg 2003); Parque Nacional Sumaco-Napo Galeras, Napo (00°23'S, 77°45'W) (Krabbe & Schulenberg 2003); Corredor Ecológico Llanganates-Sangay, Tungurahua (01°26'S, 78°10' W) (Krabbe & Schulenberg 2003); Tapichalaca Biological Reserve (details above) (Greeney & Sornoza 2005). WEST ANDES, COLOMBIA: La Linda, Jardín, Antioquia (05°38'N, 75°48'W, 2,400–2,700 m) (Cuervo *et al.* 2003). Páramo Frontino, Antioquia (06°27'N, 76°05'W, 3,300 m; 06°26'N, 76°05'W, 3,150 m) (Krabbe *et al.* 2007). CENTRAL ANDES, COLOMBIA: Cuenca del Río Toche (04°36'N, 75°24'W) (IAVH). HEAD OF MAGDALENA VALLEY, COLOMBIA: Parque Nacional Natural Cueva de los Guácharos, Huila (01°36'N, 76°08'W) (IAVH); Serranía de las Minas, Boyacá (02°10'N, 76°11'W) (IAVH).
- G. n. nana* EAST ANDES, COLOMBIA: Bosques de la Falla del Tequendama, Cundinamarca (04°43'N, 74°22'W) (IAVH); Vereda Las Minas, Huila (06°04'N, 73°00'W) (IAVH).
- G. n. kukenamensis* TEPUI: VENEZUELA: Ptari-tepui, Cerro Cuquenán, Roraima (04°45'N, 61°30'W) (Hilty 2003). GUYANA: Mt. Roraima (05°16'N, 60°44'W, 1,300 m) (Braun *et al.* 2003).
- G. n. nanitaea* MÉRIDA, VENEZUELA: Cuevas de Carache, Trujillo (09°38'N, 70°14'W) (Hilty 2003).

Note: an extralimital sight record of *G. n. olivascens* at Cerro Tucuito, Miranda / Anzoátegui, Venezuela (10°00'N, 65°39'W, 550 m) (C. Parrish *in litt.* 2008; Hilty 2003) is not included pending confirmation, as confusion with *G. ferrugineipectus*, which is known from specimens taken nearby, is possible.

APPENDIX 2: Biometrics of *Grallaricula nana* and *G. ferrugineipectus* taxaData are presented as follows: mean \pm standard deviation (n = number of specimens or individuals).

Taxon	Wing-chord from skins (mm)	Tail (mm)	Tarsus (mm)	Culmen (mm)	Bill-width (mm)	Body mass (g)
<i>G. n. occidentalis?</i> West Andes, Colombia	68.9 \pm 1.7 (66.0–72.0) ($n=37$)	34.3 \pm 3.0 (28.0–38.8) ($n=30$)	30.8 \pm 1.2 (27.5–33.4) ($n=30$)	16.8 \pm 1.7 (13.8–18.8) ($n=29$)	4.5 \pm 0.2 (4.2–4.6) ($n=4$)	20.2 \pm 0.9 (18.5–22.0) ($n=34$)
<i>G. n. occidentalis</i> Central Andes, Colombia	68.0 \pm 2.3 (63.5–71.0) ($n=15$)	33.8 \pm 3.0 (30.0–38.0) ($n=10$)	29.8 \pm 1.1 (27.9–31.4) ($n=12$)	16.0 \pm 0.5 (14.9–16.8) ($n=11$)	4.4 \pm 0.4 (4.0–5.0) ($n=8$)	20.7 \pm 0.8 (19.9–22.0) ($n=6$)
<i>G. n. occidentalis</i> Ecuador	68.8 \pm 2.3 (66.0–71.0) ($n=5$)	33.2 \pm 0.8 (32.0–34.0) ($n=5$)	29.4 \pm 0.5 (29.0–30.0) ($n=5$)	16.0 \pm 0.6 (15.5–16.5) ($n=4$)	4.0 \pm 0.1 (3.9–4.0) ($n=4$)	—
<i>G. n.</i> subsp.? head of Magdalena Valley, Colombia	63.8 \pm 0.4 (63.5–64.0) ($n=2$)	31.7 \pm 2.3 (30.0–33.3) ($n=2$)	29.8 \pm 1.1 (29.0–30.5) ($n=2$)	16.0 \pm 0.0 (16.0–16.0) ($n=2$)	4.6 \pm 0.0 (4.6–4.6) ($n=2$)	20.0 ($n=1$)
<i>G. n. nana</i> Picachos, Colombia	62.7 \pm 1.5 (61.0–64.0) ($n=3$)	32.5 \pm 0.7 (32.0–33.0) ($n=2$)	30.3 \pm 0.3 (30.0–30.5) ($n=3$)	15.7 \pm 0.3 (15.5–16.0) ($n=3$)	—	—
<i>G. n. nana</i> East Andes, Colombia	68.7 \pm 1.2 (68.0–71.0) ($n=6$)	31.3 \pm 1.2 (30.0–32.0) ($n=3$)	29.8 \pm 1.1 (28.0–31.0) ($n=5$)	15.9 \pm 0.2 (15.5–16.0) ($n=5$)	4.4 \pm 0.4 (3.9–5.0) ($n=6$)	—
<i>G. n. hallsi</i> Yariquíes, Colombia	70.0 \pm 2.6 (68.0–73.0) ($n=3$)	32.3 \pm 0.6 (32.0–33.0) ($n=3$)	31.0 \pm 0.9 (30.5–32.0) ($n=3$)	15.8 \pm 0.8 (15.0–16.5) ($n=3$)	5.0 \pm 0.2 (4.9–5.2) ($n=3$)	20.4 \pm 2.4 (18.4–23.0) ($n=3$)
<i>G. n. nanitaea</i> Tamá (Colombia–Venezuela)	66.9 \pm 3.2 (61.0–73.0) ($n=11$)	33.5 \pm 0.9 (32.0–35.0) ($n=10$)	29.2 \pm 0.9 (27.5–30.5) ($n=10$)	15.7 \pm 0.8 (15.0–17.0) ($n=9$)	4.8 \pm 0.5 (4.2–5.1) ($n=3$)	19.4 \pm 2.1 (18.0–23.0) ($n=5$)
<i>G. n. nanitaea</i> Mérida, Venezuela	67.4 \pm 2.3 (63.0–73.0) ($n=20$)	32.8 \pm 1.8 (29.5–35.5) ($n=18$)	30.2 \pm 1.1 (27.5–32.0) ($n=20$)	16.3 \pm 1.0 (14.0–18.5) ($n=20$)	4.0 \pm 0.1 (3.9–4.2) ($n=10$)	—
<i>G. n. olivascens</i> Coastal Cordillera, Venezuela	65.3 \pm 2.4 (61.0–70.0) ($n=22$)	34.0 \pm 1.4 (31.5–37.0) ($n=20$)	29.9 \pm 1.1 (28.0–32.0) ($n=21$)	16.0 \pm 0.9 (14.5–17.5) ($n=20$)	3.6 \pm 0.1 (3.5–3.7) ($n=5$)	—
<i>G. n. cumanensis</i> Caripe, Venezuela	63.0 \pm 2.3 (60.0–65.0) ($n=6$)	26.9 \pm 1.3 (25.0–28.5) ($n=6$)	25.4 \pm 1.4 (23.0–26.5) ($n=5$)	16.4 \pm 0.8 (15.5–17.0) ($n=4$)	5.4 \pm 0.2 (5.3–5.7) ($n=4$)	—
<i>G. n. pariae</i> Paria, Venezuela	63.1 \pm 2.0 (60.0–67.0) ($n=26$)	27.6 \pm 0.9 (26.0–29.5) ($n=25$)	24.6 \pm 1.0 (22.5–26.5) ($n=25$)	17.2 \pm 0.6 (16.0–18.5) ($n=25$)	6.0 \pm 0.2 (5.6–6.3) ($n=23$)	—
<i>G. n. kuenamensis</i> tepuis, Venezuela–Guyana	64.5 \pm 2.0 (60.0–68.0) ($n=21$)	28.5 \pm 1.7 (25.0–31.5) ($n=21$)	23.7 \pm 0.7 (23.0–25.0) ($n=21$)	16.2 \pm 0.4 (15.5–17.0) ($n=19$)	5.2 \pm 0.3 (4.8–5.5) ($n=17$)	—
<i>G. f. ferrugineipectus</i> Venezuela	63.9 \pm 1.6 (61.0–67.0) ($n=14$)	30.7 \pm 1.6 (29.0–34.0) ($n=13$)	22.5 \pm 0.9 (21.0–23.0) ($n=14$)	15.8 \pm 0.5 (15.0–16.5) ($n=13$)	5.3 \pm 0.4 (5.0–5.6) ($n=2$)	15.0 ($n=1$)
<i>G. f. rara</i> Colombia / Venezuela	63.0 \pm 1.7 (60.0–66.0) ($n=13$)	30.6 \pm 1.3 (29.0–33.0) ($n=14$)	23.0 \pm 0.9 (21.0–24.0) ($n=14$)	16.0 \pm 0.7 (15.0–17.0) ($n=13$)	5.0 ($n=1$)	—
<i>G. f.</i> subsp. Colombia	67.5 \pm 0.8 (66.0–68.0) ($n=6$)	31.0 \pm 1.7 (29.0–33.0) ($n=6$)	22.8 \pm 0.6 (22.0–23.0) ($n=7$)	16.4 \pm 0.4 (16.0–17.0) ($n=5$)	—	17.2 \pm 0.8 (16.0–18.0) (d.f.=4)
<i>G. cucullata</i> Colombia	69.8 \pm 2.0 (68.0–72.0) ($n=5$)	28.6 \pm 2.2 (29.0–31.0) ($n=5$)	24.1 \pm 0.9 (23.0–25.2) ($n=5$)	14.1 \pm 1.1 (13.0–15.5) ($n=5$)	5.1 \pm 0.1 (5.0–5.2) ($n=3$)	18.4 \pm 0.2 (18.2–18.5) ($n=2$)

APPENDIX 3: Vocal data for *Grallaricula nana* taxa

Songs

For each taxon / song, data are presented as follows: mean \pm standard deviation (n = number of songs analysed).

Taxon	No. of notes	Song duration (s)	Song speed (notes/s)	Max. frequency of highest note (kHz)	Frequency variation (kHz)	Change of speed	Position of peak	Note shape
<i>G. n. occidentalis?</i> West Andes, Colombia	20.54 \pm 2.54 (15–23) (n =13)	2.21 \pm 0.28 (1.55–2.52) (n =13)	9.32 \pm 0.88 (8.49–10.95) (n =13)	3.62 \pm 0.15 (3.45–3.99) (n =13)	0.71 \pm 0.14 (0.51–0.97) (n =13)	2.38 \pm 0.50 (1.83–3.50) (n =11)	0.21 \pm 0.04 (0.18–0.31) (n =13)	'Blobs': down and up
<i>G. n. occidentalis</i> Central Andes, Colombia	16.94 \pm 3.14 (10–26) (n =35)	1.76 \pm 0.25 (1.15–2.60) (n =43)	9.50 \pm 0.78 (8.13–10.81) (n =35)	3.53 \pm 0.10 (3.30–3.78) (n =43)	0.51 \pm 0.13 (0.25–0.91) (n =43)	1.69 \pm 0.38 (1.19–2.88) (n =34)	0.23 \pm 0.07 (0.02–0.36) (n =36)	'Blobs': upward, flat, u and n
<i>G. n. occidentalis</i> Ecuador & Peru	16.77 \pm 1.97 (13–22) (n =48)	1.73 \pm 0.20 (1.35–2.20) (n =51)	9.64 \pm 0.82 (7.91–11.31) (n =48)	3.65 \pm 0.18 (3.37–3.94) (n =51)	0.57 \pm 0.18 (0.31–1.10) (n =51)	1.63 \pm 0.27 (1.06–2.18) (n =46)	0.21 \pm 0.05 (0.11–0.35) (n =50)	'Blobs': up, flat, n and u (a Peru recording: upstrokes)
<i>G. n. subsp.?</i> head of Magdalena Valley, Colombia	14.67 \pm 1.12 (13–16) (n =9)	1.69 \pm 0.14 (1.52–1.87) (n =9)	8.68 \pm 0.45 (8.34–9.87) (n =9)	3.40 \pm 0.05 (3.31–3.48) (n =9)	0.53 \pm 0.09 (0.37–0.63) (n =9)	1.61 \pm 0.13 (1.45–1.78) (n =9)	0.27 \pm 0.04 (0.19–0.32) (n =9)	'Blobs': down, flat and n
<i>G. n. nana</i> Picachos, Colombia	19.67 \pm 0.58 (19–20) (n =3)	1.99 \pm 0.06 (1.95–2.06) (n =3)	9.88 \pm 0.27 (9.72–10.20) (n =3)	3.30 \pm 0.01 (3.29–3.30) (n =3)	0.51 \pm 0.09 (0.44–0.61) (n =3)	1.62 \pm 0.42 (1.33–2.10) (n =3)	0.25 \pm 0.04 (0.21–0.30) (n =3)	'Blobs': flat and up
<i>G. n. nana</i> East Andes, Colombia	16.84 \pm 3.75 (11–22) (n =19)	1.73 \pm 0.31 (1.33–2.20) (n =21)	9.46 \pm 0.61 (8.21–10.18) (n =19)	3.21 \pm 0.09 (3.02–3.38) (n =21)	0.47 \pm 0.11 (0.26–0.63) (n =21)	1.57 \pm 0.27 (1.19–2.10) (n =15)	0.25 \pm 0.05 (0.18–0.35) (n =21)	'Blobs': up, down, flat and u
<i>G. n. hallsi</i> Yariguies, Colombia	13.53 \pm 1.19 (12–16) (n =15)	1.32 \pm 0.11 (1.15–1.59) (n =15)	10.26 \pm 0.71 (9.23–11.76) (n =15)	3.27 \pm 0.02 (3.23–3.31) (n =15)	0.22 \pm 0.05 (0.13–0.33) (n =15)	1.31 \pm 0.16 (1.12–1.59) (n =12)	0.17 \pm 0.05 (0.10–0.23) (n =15)	'Blobs': up and flat
<i>G. n. nanitaea</i> Tamá (Colombia– Venezuela)	19.85 \pm 2.34 (13–23) (n =13)	1.81 \pm 0.28 (1.27–2.15) (n =17)	10.40 \pm 0.75 (9.05–11.29) (n =13)	3.73 \pm 0.08 (3.56–3.85) (n =18)	0.45 \pm 0.12 (0.23–0.62) (n =18)	1.88 \pm 0.62 (0.99–2.78) (n =9)	0.20 \pm 0.05 (0.14–0.29) (n =15)	'Blobs': flat, up and down
<i>G. n. nanitaea</i> Mérida, Venezuela	25.88 \pm 4.16 (17–32) (n =25)	2.21 \pm 0.32 (1.40–2.80) (n =25)	11.71 \pm 0.86 (10.43–13.18) (n =25)	3.84 \pm 0.20 (3.35–4.17) (n =25)	0.72 \pm 0.14 (0.33–0.97) (n =25)	1.16 \pm 0.33 (0.68–2.29) (n =24)	0.18 \pm 0.03 (0.13–0.26) (n =25)	'Blobs': up, down (some long 'tails'), n and flat
<i>G. n. olivascens</i> Coastal Cordillera, Venezuela	31.75 \pm 5.57 (17–41) (n =20)	2.17 \pm 0.40 (1.22–2.75) (n =23)	14.66 \pm 0.87 (13.21–16.50) (n =20)	3.74 \pm 0.18 (3.34–3.96) (n =24)	0.74 \pm 0.22 (0.38–1.24) (n =23)	1.36 \pm 0.29 (1.06–2.05) (n =19)	0.17 \pm 0.04 (0.10–0.22) (n =23)	'Blobs': up, down, flat and u (some 'tails')
<i>G. n. cumanensis</i> Caripe, Venezuela	33.73 \pm 4.77 (25–38) (n =11)	1.90 \pm 0.27 (1.49–2.15) (n =13)	17.78 \pm 0.56 (16.82–18.78) (n =11)	2.84 \pm 0.09 (2.69–2.98) (n =13)	0.32 \pm 0.10 (0.18–0.45) (n =13)	1.08 \pm 0.05 (1.00–1.15) (n =12)	0.34 \pm 0.04 (0.29–0.42) (n =13)	'Blobs': down with long 'tails'
<i>G. n. pariae</i> Paria, Venezuela	32.83 \pm 1.59 (29–35) (n =12)	1.85 \pm 0.10 (1.60–2.00) (n =12)	17.73 \pm 0.31 (17.30–18.33) (n =12)	2.71 \pm 0.05 (2.63–2.76) (n =12)	0.33 \pm 0.09 (0.18–0.44) (n =12)	1.11 \pm 0.06 (1.02–1.20) (n =12)	0.36 \pm 0.04 (0.27–0.41) (n =12)	'Blobs': down with long 'tails'
<i>G. n. kukenamensis</i> tepuis, Venezuela	69 (n =1)	5.07 (n =1)	13.61 (n =1)	3.55 (n =1)	0.80 (n =1)	0.96 (n =1)	0.18 (n =1)	Chevron
<i>G. f. ferrugineipectus</i> Mérida, Venezuela	17.10 \pm 2.51 (12–20) (n =11)	2.10 \pm 0.27 (1.50–2.41) (n =11)	8.13 \pm 0.76 (6.92–9.71) (n =11)	2.63 \pm 0.13 (2.36–2.77) (n =11)	0.48 \pm 0.30 (0.21–0.97) (n =11)	0.98 \pm 0.19 (0.78–1.35) (n =11)	0.69 \pm 0.07 (0.51–0.80) (n =11)	'Blobs': up and down
<i>G. lineifrons</i> Ecuador & Peru	16.43 \pm 2.31 (10–20) (n =30)	2.92 \pm 0.41 (1.69–3.45) (n =30)	5.64 \pm 0.24 (5.14–6.09) (n =30)	4.73 \pm 0.19 (4.42–5.21) (n =30)	1.30 \pm 0.22 (0.86–1.72) (n =30)	0.96 \pm 0.10 (0.72–1.14) (n =30)	0.88 \pm 0.09 (0.69–1.00) (n =30)	Chevron
<i>G. cucullata</i> Colombia	25.11 \pm 4.34 (16–32) (n =9)	1.84 \pm 0.30 (1.23–2.40) (n =11)	14.0 \pm 0.70 (13.00–14.81) (n =9)	4.40 \pm 0.07 (4.29–4.55) (n =11)	0.64 \pm 0.09 (0.55–0.88) (n =11)	1.11 \pm 0.19 (0.77–1.48) (n =9)	0.39 \pm 0.11 (0.28–0.57) (n =11)	Chevron

Calls

For each taxon / call, data are presented as follows: mean \pm standard deviation (n = number of calls analysed). No recordings were available for the West Andes or head of the Magdalena Valley populations.

Taxon	No. of notes	Call duration (s)	Call speed (notes/s)	Max. frequency of highest note (kHz)	Frequency variation (kHz)	Change of speed	Position of peak	Note shape
<i>G. n. occidentalis</i> Central Andes, Colombia	1 (all) ($n=12$)	0.15 \pm 0.02 (0.12–0.18) ($n=12$)	n/a	4.08 \pm 0.31 (3.56–4.50) ($n=12$)	n/a	n/a	n/a	Downstroke, some broken; flat notes
<i>G. n. occidentalis</i> Ecuador & Peru	1 (all) ($n=11$)	0.10 \pm 0.01 (0.08–0.12) ($n=11$)	n/a	4.30 \pm 0.26 (3.90–4.66) ($n=11$)	n/a	n/a	n/a	Downstrokes
<i>G. n. nana</i> Picachos, Colombia	1 (all) ($n=3$)	0.11 \pm 0.00 (0.11–0.11) ($n=3$)	n/a	3.71 \pm 0.09 (3.62–3.80) ($n=3$)	n/a	n/a	n/a	Flat notes
<i>G. n. nana</i> East Andes, Colombia	1 (all) ($n=3$)	0.11 \pm 0.01 (0.11–0.13) ($n=3$)	n/a	3.85 \pm 0.01 (3.85–3.86) ($n=3$)	n/a	n/a	n/a	Flat notes
<i>G. n. hallsi</i> Yariguies, Colombia	1 (all) ($n=7$)	0.12 \pm 0.01 (0.12–0.14) ($n=7$)	n/a	4.23 \pm 0.22 (3.85–4.49) ($n=7$)	n/a	n/a	n/a	Downstroke, some broken
<i>G. n. nanitaea</i> Tamá (Colombia– Venezuela)	1 (all) ($n=3$)	0.13 \pm 0.00 (0.13–0.13) ($n=3$)	n/a	4.73 \pm 0.11 (4.60–4.80) ($n=3$)	n/a	n/a	n/a	Sharp note
<i>G. n. nanitaea</i> Mérida, Venezuela	1 (all) ($n=3$)	0.11 \pm 0.01 (0.10–0.12) ($n=3$)	n/a	4.81 \pm 0.02 (4.79–4.82) ($n=3$)	n/a	n/a	n/a	Downstroke
<i>G. n. olivascens</i> Coastal Cordillera, Venezuela	1 (all) ($n=14$)	0.14 \pm 0.02 (0.10–0.17) ($n=14$)	n/a	4.71 \pm 0.19 (4.48–5.14) ($n=14$)	n/a	n/a	n/a	Downstroke, some broken
<i>G. n. cumanensis</i> Caripe, Venezuela	Trills: 5.40 \pm 0.55 (5–6) ($n=5$) Notes within a single trill: 6.60 \pm 2.59 (3–11) All notes in series of trills: 33.00 \pm 4.36 (28–36)	Total: 0.86 \pm 0.07 (0.79–0.95) ($n=5$) For individual trills: 0.12 \pm 0.15 (0.05–0.21)	Trills per second: 6.27 \pm 0.20 (6.00–6.55) ($n=5$) Within trills: 58.40 \pm 3.97 (53.40–65.21)	3.45 \pm 0.07 (3.35–3.53) ($n=5$)	0.26 \pm 0.23 (0.05–0.65) ($n=5$)	1.60 \pm 0.15 (1.39–1.81) ($n=5$)	0.87 \pm 0.18 (0.60–1.00) ($n=5$)	Series of short, fast trills
<i>G. n. pariae</i> Paria, Venezuela	Trills: 4.24 \pm 2.05 (2–8) ($n=17$) Notes within a single trill: 5.25 \pm 2.83 (2–11) All notes in series of trills: 19.29 \pm 7.19 (13–34)	For series of trills: 0.73 \pm 0.27 (0.39–1.22) ($n=17$) For individual trills: 0.13 \pm 0.07 (0.05–0.29)	Trills per second: 5.54 \pm 0.80 (4.26–6.57) ($n=17$) Within trills: 41.01 \pm 3.55 (34.48–49.55)	3.60 \pm 0.12 (3.34–3.76) ($n=17$)	0.32 \pm 0.11 (0.03–0.46) ($n=17$)	1.65 \pm 0.47 (0.79–2.40) ($n=17$)	0.20 \pm 0.21 (0.00–0.84) ($n=17$)	Series of short, fast trills
<i>G. n. kukenamensis</i> tepuis, Venezuela	1 (or very fast 3- note trill?) ($n=3$)	0.08 ($n=1$)	n/a	3.48 ($n=1$)	n/a	n/a	n/a	Broken downstroke / of three rapid notes

<i>G. n. occidentalis?</i> (West Andes)	<i>G. n. occidentalis</i> (Central Andes)(Ecuador)	<i>G. n. nana</i> (East Andes)	<i>G. n. hallsi</i> (Yariguáes)	<i>G. n. namitaca</i> (Tamá-Santander)	<i>G. n. namitaca</i> (Mérida)	<i>G. n. olivaceus</i> (Coastal Cordillera)	<i>G. n. cumanaensis</i> (Caripe)	<i>G. n. pariae</i> (Paría)	<i>G. kaikenansis</i> (tepuís)
<i>G. n. namitaca</i> (Tamá-Santander)	<i>G. n. occidentalis?</i> More olivaceous back paler breast	<i>G. n. nana</i> More olivaceous back, paler breast	<i>G. n. hallsi</i> BW(1,2,4,5)	<i>G. n. namitaca</i> X	<i>G. n. namitaca</i> SL(1) NN(1) SS(1) FV(1)	<i>G. n. olivaceus</i> SL(1) NN(1,2) SS(1,2,3,4,5) FV(1)	<i>G. n. cumanaensis</i> NN(1,2,4) SS(1,2,3,4,5) MF(1,2,3,4,5) FV(1) CP(1,2) PP(1,2,4) NS(4)	<i>G. n. pariae</i> NN(1,2,3,4,5) SS(1,2,3,4,5) MF(1,2,3,4,5) FV(1) CP(1,2) PP(1,2,3) NS(4)	<i>G. kaikenansis</i> NN(2,4,5) SL(2,4,5) NS(4)
<i>G. n. namitaca</i> (Mérida)	More olivaceous back paler breast	More olivaceous back, paler breast	More olivaceous back, paler breast	More olivaceous back, paler breast	X	NN(1) NN(1,2) SS(1,2,3,4)	SL(1) NN(1,2) SS(1,2,3,4,5) MF(1,2,3,4,5) FV(1,2) PP(1,2,3,4,5) NS(4)	NN(1,2,3,4,5) SS(1,2,3,4,5) MF(1,2,3,4,5) FV(1) CP(1,2) PP(1,2,3) NS(4)	NN(2,4,5) SL(2,4,5) NS(4)
<i>G. n. olivaceus</i> (Coastal Cordillera)	More olivaceous back, paler breast	More olivaceous back, paler breast	More olivaceous back, paler breast	More olivaceous back, paler breast	X	NN(1,2,3,4,5) SL(1,2,4) X	SL(1) NN(1,2) SS(1,2,3,4,5) MF(1,2,3,4,5) FV(1,2) PP(1,2,3,4,5) NS(4)	NN(1,2,4,5) SL(1,2,4) MF(1,2,3,4,5) NS(4)	NN(2,4,5) SL(2,4,5) NS(4)
<i>G. n. cumanaensis</i> (Caripe)	More olivaceous back, paler breast	More olivaceous back, paler breast	More olivaceous back, paler breast	More olivaceous back, paler breast	X	SS(1,2,3,4,5) MF(1,2,3,4,5) FV(1,2) PP(1,2,3,4,5)	SS(1,2,3,4,5) MF(1,2,3,4,5) FV(1,2) PP(1,2,3,4,5)	SS(1) SS(1,2,3,4,5) MF(1,2,3,4,5) FV(1,2) PP(1,2,3,4,5)	NN(2,4,5) SL(2,4,5) NS(4)
<i>G. n. pariae</i> (Paría)	More olivaceous back, paler breast	More olivaceous back, paler breast	More olivaceous back, paler breast	More olivaceous back, paler breast	X	NN(1,2,3,4,5) SL(1,2,3,4,5) MF(1,2,3,5) NS(4)	NN(1,2,3,4,5) SL(1,2,3,4,5) MF(1,2,3,5) NS(4)	NN(1,2,4,5) SL(1,2,4) MF(1,2,3,4,5) NS(4)	MF(2,5)
<i>G. kaikenansis</i> (tepuís)	More olivaceous back, paler breast	More olivaceous back, paler breast	More olivaceous back, paler breast	More olivaceous back, paler breast	X	MF(1)	MF(1)	MF(1)	NN(2,4,5) SS(2,4,5) MF(2,4,5) SL(2,4,5) NS(4) FV(2) PP(2)
<i>G. n. olivaceus</i> (Caripe)	More olivaceous back, paler breast	More olivaceous back, paler breast	More olivaceous back, paler breast	More olivaceous back, paler breast	X	SS(1) TL(1,2,3,4,5) SL(1,2,3,4,5) TR(1,2,4)	SS(1) TL(1,2,3,4,5) SL(1,2,3,4,5) TR(1,2,4)	SS(1,2,3,4,5) MF(1)	NN(2,4) SL(2) NS(4)
<i>G. n. pariae</i> (Paría)	More olivaceous back, paler breast	More olivaceous back, paler breast	More olivaceous back, paler breast	More olivaceous back, paler breast	X	W(1) TL(1,2,4) X	W(1) TL(1,2,4) X	W(1) TL(1,2,3,4,5) SL(1,2,3,4,5) BS(4)	W(1) TL(1,2,3,4,5) SL(1,2,3,4,5) BS(4)
<i>G. kaikenansis</i> (tepuís)	More olivaceous back, paler breast	More olivaceous back, paler breast	More olivaceous back, paler breast	More olivaceous back, paler breast	X	W(1) TL(1,2,4) X	W(1) TL(1,2,4) X	W(1) TL(1,2,3,4,5) SL(1,2,3,4,5) BS(4)	W(1) TL(1,2,3,4,5) SL(1,2,3,4,5) BS(4)
<i>G. n. pariae</i> (Paría)	More olivaceous back, paler breast	More olivaceous back, paler breast	More olivaceous back, paler breast	More olivaceous back, paler breast	X	W(1) TL(1,2,4) X	W(1) TL(1,2,4) X	W(1) TL(1,2,3,4,5) SL(1,2,3,4,5) BS(4)	W(1) TL(1,2,3,4,5) SL(1,2,3,4,5) BS(4)
<i>G. kaikenansis</i> (tepuís)	More olivaceous back, paler breast	More olivaceous back, paler breast	More olivaceous back, paler breast	More olivaceous back, paler breast	X	W(1) TL(1,2,4) X	W(1) TL(1,2,4) X	W(1) TL(1,2,3,4,5) SL(1,2,3,4,5) BS(4)	W(1) TL(1,2,3,4,5) SL(1,2,3,4,5) BS(4)
<i>G. n. pariae</i> (Paría)	More olivaceous back, paler breast	More olivaceous back, paler breast	More olivaceous back, paler breast	More olivaceous back, paler breast	X	W(1) TL(1,2,4) X	W(1) TL(1,2,4) X	W(1) TL(1,2,3,4,5) SL(1,2,3,4,5) BS(4)	W(1) TL(1,2,3,4,5) SL(1,2,3,4,5) BS(4)
<i>G. kaikenansis</i> (tepuís)	More olivaceous back, paler breast	More olivaceous back, paler breast	More olivaceous back, paler breast	More olivaceous back, paler breast	X	W(1) TL(1,2,4) X	W(1) TL(1,2,4) X	W(1) TL(1,2,3,4,5) SL(1,2,3,4,5) BS(4)	W(1) TL(1,2,3,4,5) SL(1,2,3,4,5) BS(4)

Less olivaceous back, darker breast, less extensive white belly and less extensive white collar, less ferruginous-red on breast, shorter eyebrow, and absence of pale postocular

Less olivaceous back, darker breast

Less olivaceous back, darker breast

Less olivaceous back, darker breast, less extensive white belly and less extensive white collar, less ferruginous-red on breast, shorter eyebrow, and absence of pale postocular

More olivaceous back, paler breast

More olivaceous back, paler breast

More olivaceous back, paler breast

More olivaceous back, paler breast